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Effects of diversity on beneficial and pest arthropods

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by

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ABSTRACT

Vegetational diversity within agroecosystems can vary in in three basic ways; the species richness of plants, the spatial arrangement of species and the temporal relationship among species. Agroecosystems with greater vegetational diversity are associated with decreased pest abundance and increased natural enemy abundance. The objectives of this dissertation were to test the effect of farming practices that alter vegetational diversity on beneficial arthropod communities and pest insects. Farming practices investigated included the addition rye cover crop (*Secale cereale* L.) to corn (*Zea mays* L.) and the use of extended crop rotations.

Two separate studies were conducted on experimental plots to compare the effects of the addition of a rye cover crop and extended crop rotations against practices that lacked diversity on epigeal and canopy, beneficial arthropod communities. In both studies we hypothesized that practices that increased vegetational diversity would positively affect beneficial arthropods. Only modest differences were observed in the composition and abundance of beneficial arthropods with the addition of a rye cover crop and none were detected among crop rotations with different lengths.

Two on-farm studies were conducted to quantify the effects rye cover crop and the use of extended crop rotations on insect pests of corn. Farming practices, corn root injury and abundance of *Diabrotica* spp. were compared among cornfields that differed in the frequency of crop rotation and previous pest injury. Root injury and abundance of *Diabrotica* spp. were similar among cornfields, however, fields that had a history of crop rotation required significantly fewer pest management inputs. In the second study, the abundance of early season insect pests and injury to corn were compared between fields with and without a rye cover crop. Although adult moths were captured around all cornfields, significantly greater abundance of *Mythimna unipuncta* and greater proportion of defoliated corn were found in fields where corn followed a rye cover crop.

CHAPTER 1.

GENERAL INTRODUCTION

Dissertation Organization

This dissertation is organized in six chapters. The first chapter is a literature review of the effects of diversity in agroecosystems on arthropods and the ecology of several key pest species. The second and third chapters discuss experiments designed to test the effects of increasing vegetational diversity in agroecosystems, the addition of rye cover crop and extended crop rotation, respectively, on beneficial arthropods. Chapters four and five describe on-farm studies investigating the effects of vegetational diversity in agroecosystems, the addition of rye cover crop and extended crop rotation, respectively, on insect pests of corn. The sixth and final chapter presents general conclusions of this project.

Literature Review

Diversity & Agroecosystems. Vegetational diversity within agroecosystems can vary in three basic ways, the kinds of plants, the spatial arrangement of species and the temporal relationship among species (Andow 1991a). Diversity of kinds of plants typically refers to different species of plants (i.e., polyculture, weedy culture, living mulches), but can also refer to diversity within the same species (i.e., mixes of Bt and non-Bt crop). Spatial diversity of vegetation can change with how plants are arranged within a given unit of space (i.e., crops planted in single species blocks or crops planted to alternate rows). Vegetational diversity also can vary temporally, with crops and non-crops overlapping completely in time (i.e., intercropping, living-mulched, weedy culture) or separated entirely by time (i.e., crop rotation). The scale at which vegetational diversity within agroecosystems is measured can

also vary. Diversity within agroecosystems can be altered by farming practices within crop fields (i.e., intercropping, cover crops, beetle banks) or by changes in landscape heterogeneity (i.e., composition and connectivity among fields).

Diversity & Pests. Agroecosystems with greater vegetational diversity are associated with decreased pest abundance (Root 1973, Andow 1991a). In a recent literature review, Letourneau et al. (2011) used data from 552 experiments that manipulated vegetational diversity to test the effect of diverse cropping schemes on the abundance of pests, crop injury and crop yield. Meta-analysis with Hedges' *d* was used to measure the overall treatment effect size (Rosenberg et al. 2000). Treatment effects are considered significant when the value of Hedges' *d* has a 95% confidence interval that excludes zero. Effect sizes that exceed 0.7 or -0.7 are considered large for insect populations (Tonhasca and Byrne 1994). More diverse cropping schemes had significant and negative effect sizes for pest abundance (d = -1.3), crop injury (d = -2.3) and crop yield (d = -0.8). Both pest abundance and crop injury were reduced by 23% when more diverse cropping schemes were compared to less diverse cropping schemes or monocultures. However, crop yields were reduced by 14% with more diverse cropping schemes. In another literature review, meta-analysis with Hedges' *d* was used to measure the effect size of purposeful manipulation of habitat complexity (i.e., leaf-litter volume or diversity, leaf density, vegetation density or diversity) on insect herbivore abundance (Langellotto and Denno 1994). However, herbivore abundance was unaffected by either increasing or decreasing habitat complexity.

There are several, non-exclusive hypotheses that explain why agroecosystems with greater diversity can reduce pest abundance. The resource concentration hypothesis predicts that lower pest abundance in diverse agroecosystems, compared to monocultures, occurs

because pests with narrow host ranges are less frequently recruited and retained in diverse agroecosystems (Root 1973). Pests may also be less frequently retained in more diverse fields because some plant associations decrease the likelihood of herbivores detecting the host plant, a plant-plant association known as associational resistance (Tahvanaien and Root 1972, Finch et al. 2003, Barbosa et al. 2009). Additionally, the host-plant quality hypothesis predicts that lower pest abundance in agroecosystems with greater vegetational diversity occurs because crops in diverse setting compete with the other crops or non-crops, resulting in decreased host quality for pest insects (Bach 1981, Bukovinszky et al. 2004).

Diversity & Natural Enemies. One of the significant ecosystem services provided by arthropods is biological control of pests (Losey and Vaughan 2006). The enemies hypothesis predicts that natural enemies such as predators and parasitoids would be more abundant in agroecosystems with greater vegetational diversity, compared to monocultures, thereby reducing pest abundance (Root 1973, Andow 1991a, Altieri 1999, Landis et al. 2000). Compared to monocultures, more diverse agroecosystem may be more hospitable to natural enemies because they can offer better alternate food resources, more favorable microclimates and refuge from environmental or anthropogenic disturbances (Marion and Landis 1996, Landis et al. 2000, Sunderland and Samu 2000, Symondson et al. 2002, Gardiner et al. 2009a).

Letourneau et al. (2011) also tested the effect of more diverse cropping schemes on the abundance natural enemies. More diverse cropping schemes had a significant and positive effect size on natural enemies (d = 1.2), which increased natural enemy abundance by 54% compared to less diverse cropping schemes or monocultures. Changes in vegetational diversity can also affect habitat structure and complexity for predators and

parasitoids. Additionally for generalist predators, habitat complexity may also provide refuge from intraguild predation or cannibalism (Wagner and Wise 1996, Rosenheim 2001, Finke and Denno 2002). Langellotto and Denno (1994) also tested the effect of habitat complexity on natural enemy abundance. The effect size of increased habitat complexity on overall natural enemy abundance was significant and positive (d = 0.87), while decreasing habitat complexity produced a significant and negative response (d = 0.64). Furthermore, increasing habit complexity by either manipulating the amount of detritus (i.e, thatch, leaf litter, mulch) or the amount of living vegetation (i.e, no-till or mowing management, intercropping, polycultures) had significant and large positive effects on natural enemy abundance (d = 2.37 and 0.69, respectively). Natural enemy response to structural diversity was also test within guilds, and the majority of guilds tested responded positively to increasing habitat complexity, including hunting and web-building Araneae, predatory Acari, predatory Hemiptera and parasitoids. Hunting and web-building Araneae, predatory Hemiptera and Formicidae abundance each significantly decreased when habitat complexity was purposefully reduced. Coccinellidae (Coleoptera) and Carabidae (Coleoptera) did not respond to either positive or negative changes in structural diversity.

Cover Crops. Cover crops are non-crop species planted prior to or intercropped with a cash crop (Hartwig and Ammon 2002). The benefits of adding a cover crop include reducing soil and nutrient loss, improving soil health, and suppressing weeds (Owens et al. 2000, Kasper et al. 2001, Hartwig and Ammon 2002). By creating a barrier over the soil surface, cover crops can increase water infiltration into the soil and decrease the movement of pesticides and nitrogen fertilizers from the field (Hall et al. 1984, Danso et al. 1991). Nitrate movement into river basins has been linked to downstream hypoxic zones (Turner et

al. 2006, Sprague et al. 2011); however, landscape-level adoption of cover crops has been shown to substantially reduce movement of nitrogen from croplands into the water table, thereby reducing negative downstream effects of excess nitrogen (USDA, NRCS 2013b).

The addition of a cover crop also increases vegetational diversity within fields (Andow 1991b). Cover crops may decrease insect pest abundance by creating habitat for natural enemies (Carmona and Landis 1999, Landis et al. 2000). *Ostrinia nubilalis* Hubner (Lepidoptera: Crambidae), European corn borer, used as sentinel prey in corn (*Zea mays* L.) and soybean (*Gylcine max* L.) plots were consumed at greater frequency in plots planted with an alfalfa (*Medicago sativa* L.) and kura clover (*Trifolium ambiguum* M. Bieb.) living-mulch cover crop than without a cover crop (Prasifka et al. 2006). Foliar predators in soybean plots were both significantly more abundant and diverse in soybean canopies when plots also included a living-mulch cover crop of alfalfa (Schmidt et al. 2007). Furthermore, *Aphis glycines* Matsumura (Hempitera: Aphididae), soybean aphid, population growth rates were lower in soybean plots with the living-mulch cover crop (Schmidt et al. 2007).

Rye Cover Crop. Rye (*Secale cerale* L.) is planted as cover crop in the U. S. Corn Belt because of its cold tolerance and rapid growth early in the spring (Stoskopf 1985, Bollero and Bullock 1994, Dinnes et al. 2002). Rye capably competes with weeds for resources such as light and moisture, and produces secondary metabolites that further suppress weed growth (Barnes and Putnam 1987, Weston and Duke 2003). Residue from destroyed rye can reduce weed biomass up to 50% (Moyer et al. 2000). The growth of weed seedbanks is positively related to weed biomass (Teasdale et al. 2003), and the addition of a rye cover crop has been shown to both reduce weed biomass (Moyer et al. 2000, Weston and Duke 2003) and weed seedbank density (Moonen and Barberi 2004).

Rye Cover Crop Management. Despite rye's benefits, adoption of rye as a cover crop throughout the Corn Belt is limited. Low adoption of rye may be explained in part by rye's cost of establishment/ termination and the risk of competition between rye and a cash crop (Tollenaar et al. 1993, De Bruin et al. 2005). A rye cover crop in the Corn Belt is typically seeded in the fall and terminated in the spring before the cash crop is planted (Clark 2007, Casey 2012; USDA, NRCS 2013a). It is recommended that rye cover crop is termination two to three weeks before corn is planted or when rye reaches 15 to 20 cm in height, whichever comes first (MCCC 2012). When corn is planted following a rye cover crop, timing of rye termination is critical to preventing negative impacts on corn development (Raimbault et al. 1990, Tollenaar et al. 1993; MCCC, 2012). Early destruction prevents rye from reaching reproductive stages, where it would immobilize nitrogen (Tollenaar et al. 1993). Additionally, early termination of rye would reduce the risk of rye becoming a weed and competing with the cash crop and the potentially negative allelopathic effects (Weston and Duke 2003, Casey 2012, MCCC 2012).

Farmers wanting to plant cover crops can receive financial add to offset the initial costs of establishing a cover crop through the Environmental Quality and Incentives Plan (EQIP) (USDA, NRCS 2015). Farmers enrolled in EQIP who plant a cover crop that is terminated chemically or mechanically (including rye) are eligible to receive $40.63 per acre for up to three years (USDA, NRCS 2015). Furthermore, farmers can attach insurance to cash crops that follows a cover crop under certain conditions (USDA, RMA 2014), one such condition being the timing of cover crop termination based on geographic zones (USDA, NRCS 2013c). The majority of the Corn Belt is classified by the cover crop termination guidelines as being in either Zone 3 or 4, and recommends termination of the cover crop at or

before planting (Zone 3) or at planting or within five days post-planting but before the cash crop emerges (Zone 4) (USDA, NRCS 2013c). Although these termination guidelines are purposefully broad in order to encompass the many combinations of cash and cover crop combinations, farmers planting corn following a rye cover crop should be made aware of the risk of late rye termination to corn development (Raimbault et al. 1990, Tollenaar et al. 1993, MCCC, 2012).

Rye Cover Crop & Arthropods. The resource concentration hypothesis predicts that insect herbivores respond negatively to increased diversification (Root 1973, Andow 1991a), and pest insect abundances has been observed to decline in fields that added rye cover crop. Organic soybean fields in Minnesota planted with and without a rye cover crop did not differ in foliar predator abundance, yet the presence of rye cover crop did reduced *Empoasca fabae* Harris (Hemiptera: Cicadellidae), potato leafhopper, *Cerotoma trifurcata* Forster (Coleoptera: Chrysomelidae), bean leaf beetle and *A. glycines* abundances (Koch et al. 2012). The addition of a rye cover crop into snap beans (*Phaseolus vulgaris* L.) had no effect on foliar predators, although the abundance of *Orius insidiosus* Say (Hempitera: Anthocoridae), insidious flower bug, was reduce when rye was combined with red clover cover crop (*Trifolium pretense* L.) (Bottenberg et al. 1997). From the same study, *E. fabae* was also reduced when snap beans were planted with a rye cover crop, though this effect was in part due to the reduced size of snap beans in plots that included rye. Reduction of pest abundance is also predicted to occur when competition among crops and non-crops within fields lower host-plant quality (Bach 1981, Bukovinszky et al. 2004). Negative effects on corn and soybean, including yield loss due to Nitrogen immobilization and stand reduction, have been

detected when rye has been added as a cover crop (Eckert 1988, Tollenaar et al. 1993, DeBruin et al. 2005).

Rye cover crop management can also alter the responses of both pests and natural enemies. Rye termination can be achieved by mechanical processes (i.e., mowing, crimping, or tillage) or terminated chemically with herbicide (Clark 2007, Casey 2012). A study measuring the effect of rye termination practices on predator activity in corn found that early season activity-densities of Lycosidae and Carabidae peaked earlier in the year when rye was destroyed by mowing compared to destruction with an herbicide (Laub and Luna 1992). Soybean insect pests also respond variably to different rye cover crop termination methods (Smith et al. 1988). The abundance of *E. fabae* was positively affected by soybeans plots that either did not have a rye cover crop or had a rye cover crop that was incorporated into the soil with disk tillage. Conversely, *Popillia japonica* Newman (Coleoptera: Scarabaeidae), Japanese beetle, and *C. trifurcata* were both significantly more abundance in soybeans plots where the rye cover crop was terminated with herbicide and left standing.

Rye Cover Crop & Polyphagous Pests. Polyphagous pests that are associated with rye have the potential to injury cash crops when rye is added as a cover crop. There are several species of noctuid moths whose host range include rye; *Mythimna unipuncta* Haworth (Lepidoptera: Noctuidae), true armyworm, *Agrotis ipsilon* Hufnagel (Lepidoptera: Noctuidae), black cutworm and *Papaipema nebris* Guenee (Lepidoptera: Noctuidae), common stalk borer. All three of these species are early-season pests of corn (Willson and Eisley 1992, Showers 1997, Rice and Davis 2010). Cultural practices that alter host-plant diversity within fields (i.e., planting a cover crop, destruction of weeds, tillage) affect population dynamics of each of these species, and injury to corn from these species typically

occurs when vegetational diversity within or around cornfields is reduced (Rice and Pedigo 1997, Showers 1997, Capinera 2008).

Mythimna unipuncta do not overwinter in the Corn Belt, but migrate northward from Gulf Coast states each year during early spring (Hendrix III and Showers 1992). Oviposition occurs on grasses and weeds before corn is planted (Capinera 2008). Extreme outbreaks of *M. unipuncta* in corn are infrequent (Guppy 1961), but occur more often in cornfields following a grassy crop (Willson and Eisley 1992, Capinera 2008). Infrequent outbreaks may be the result of *M. unipuncta* being readily attacked by a suite of natural enemies as well as being highly susceptible to cytoplasmic polyhedrosis (Reoviridae) and nuclear polyhedrosis (Baculovirirdae) viruses (Marion and Landis 1996, Capinera 2008). Sporadic outbreaks make preventative management of *M. unipuncta* difficult, especially as there are no commercially available Bt toxins that target *M. unipuncta* (Cullen et al. 2013). Therapeutic management of *M. unipuncta* is possible. Farmers can scout fields for signs of larvae and larvae feeding and apply foliar insecticides as needed (Harrison et al. 1980).

Agrotis ipsilon also does not overwinter in the Corn Belt and migrates northward from Gulf Coast states during early spring (Hendrix III and Showers 1992). Female *A. ipsilon* oviposit on low-lying weeds and fine-textured plant debris (Showers 1997). *Agrotis ipsilon* are highly polyphagous and larvae can develop on several species of weeds even more successfully than they can on corn (Showers 1997). Injury to corn from *A. ipsilon* is associated with reduced tillage or no tillage management (Willson and Eisley 1992). Additionally, weed management in cornfields can affect the risk of injury to corn from *A. ipsilon*. Having weeds within cornfields can reduce the risk of injury to corn from *A. ipsilon* (Mulder and Showers 1983), and larvae should starve if weeds are destroying more than 2

weeks before corn is planted (Showers et al. 1985). At present there are two Bt toxins that target *A. ipsilon*; Vip3A (event MIR162) and Cry1F (event TC1507) (Cullen et al. 2013).

Unlike *A. ipsilon* and *M. unipuncta*, *P. nebris* do successfully overwinter in the northern Corn Belt. Female *P. nebris* oviposit on dead vegetation in the fall, preferentially on thin-stemmed, perennial grasses over annual, wide-leaved grasses (such as rye) or broad-leaved plants (Levine 1985, Highland and Roberts 1989, Rice and Davis 2010). Although rye is not a preferred ovipositional substrate, larvae will readily feed and tunnel into rye plants (Highland and Roberts 1987). Injury to corn attributed to *P. nebris* is normally limited to field margins where corn is found adjacent to grass waterways, ditches, or terraces (Davis and Pedigo 1990, Meyer and Peterson 1998). Destruction of weedy host plants can facilitate *P. nebris* movement into cornfields (Levine 1993), but developing *P. nebris* larvae can outgrow host plants and move to larger hosts, including corn (Lasack and Pedigo 1986). Only one Bt toxin is presently labeled for *P. nebris*, Vip3A (event MIR162) (Cullen et al. 2013).

Crop Rotation. Crop rotation alters agroecosystem diversity, both spatially and temporally, and is associated with numerous agronomic benefits. Annual rotation of corn and soybean can significantly increase corn yield compared to corn planted continuously, even after continuous corn received increasing rates of fertilizers and pesticide are applied (Bullock 1992). Adding additional crops to rotation schemes can further increase yields and reduce reliance on chemical inputs (Smith et al. 2008). For example, conventionally managed corn and soybean in annual rotation was not as profitable or productive compared to an extended three-year rotation that added small grains (oat (*Avena sativa* L.) or spring triticale (*Triticosecale* L.)) or a four-year rotation that added small grains and alfalfa (Davis et al. 2012).

The expansion of monocultures typically resulted in the loss of spatial diversity and the reduction of natural habitats (Altieri and Letourneau 1982). Increasing the diversity of crops within rotation schemes would correspondingly increase agroecosystem diversity, particularly in the U.S. Corn Belt which is dominated by production of corn and soybean (USDA, NASS 2015). Low crop diversity and increased farming efficiency together limit the heterogeneity of crop management practices and promote temporal uniformity among fields (Benton et al. 2003). O'Rourke et al. (2008) compared Carabidae communities between annually rotated corn and soybean with conventional chemical inputs and a four-year rotation of corn, soybean, spring triticale/ alfalfa, alfalfa with minimal inputs. Carabidae assemblage activity-density and species richness were significantly greater when sampled from the four-year rotation plots, although Simpson's diversity did not differ between rotation treatments and Simpson's evenness was significantly greater in the two-year rotation plots. Within the Corn Belt, more diverse landscapes provided greater biological control of *A. glycines* compared to landscapes that were predominately corn and soybean (Gardiner et al. 2009a). *Aphis glycines* predators, which were principle Coccinellidae, were more abundant when the composition of landscapes within a 1.5 km area surrounding focal soybean fields included abundant forests and grasslands as opposed to landscapes dominated by agriculture. Additionally, landscape vegetational diversity and structure also influenced the composition of *A. glycines* predator communities, with native Coccinellidae found in greater abundance in low-diversity landscapes composed of grassland and exotic Coccinellidae found in greater abundance in forested landscapes (Gardiner et al. 2009b).

If additional crop species added to rotation schemes are annual crops then agroecosystems may remain temporally unstable and subject to anthropogenic disturbances.

Management practices associated with annual crops (i.e., planting, tillage, harvesting, pesticide applications) regularly disturb habitat and disrupt the effectiveness of natural enemies (Altieri 1999, Landis et al. 2000) and other types of beneficial arthropods, including granivores and detritivores (Robertson et al. 1994, Cromar et al. 1999, Baraibar et al. 2009). It is thought that the addition of perennial crops or non-crops to rotation schemes and increased connectivity among more stable habitats would support more robust natural enemy communities (Altieri and Letourneau 1982, Altieri 1999, Landis et al. 2000). For example, natural enemies overwinter more often in field margins because they provide better overwintering shelter than bare crop fields (Thomas et al. 1992a). Strips of perennial grasses planted throughout agricultural fields (beetle banks) have been shown to increase the availability of stable habitats for predators and increase predator movement throughout fields (Thomas et al. 1992b). Granivores are also affected by disturbance regimes, and post dispersal predation of weed seeds by arthropods can be negatively affected by management practices such as tillage (Cromar et al. 1999).

There are potential negative effects associated with crop rotation. Primarily, increasing diversity within crop rotations can reduce the area planted to high value crops (Landis et al. 2000). This drawback can be compounded if extended rotations include non-crop species (Altieri 1994).

Diabrotica v. virgifera. *Diabrotica virgifera virgifera* LeConte (Coleoptera: Chrysomelidae), western corn rootworm, is a significant pest of corn in North America. Economic losses attributed to the cost of *D. v. virgifera* management and yield lost are estimated to exceed $1 billion annually (Metcalf 1986, Rice 2004, Gray et al. 2009). *Diabrotica v. virgifera* are univoltine with a life cycle that is tightly associated with corn,

their host plant (Meinke et al. 2009, Spencer et al. 2009). Adult *D. v. virgifera* feed on corn silks, pollen and kernels. Eggs are oviposited in the soil of cornfields during late summer and early fall, diapause through the winter and larvae hatch in the spring. Larvae feed on corn roots and feeding injury reduces the ability of plants to take up water and nutrients (Levine and Oloumi-Sadeghi 1991). Larvae feeding on corn roots is the primary cause of yield loss from *D. v. virgifera* (Gray et al. 2009), and corn yield is reduced by 15% for each node of root injured (Tinsley et al. 2013).

Management of *D. v. virgifera.* Mitigating *D. v. virgifera* injury to corn can be difficult as this pest has evolved resistance to several management tactics. Presently, commercial corn hybrids with effective host plant resistance to *D. v. virgifera*, excluding genetically modified plants, are not available (Khishen et al. 2009). There is evidence that biologic control via entomopathogens can help reduce root injury from *D. v. virgifera* (Hiltpold et al. 2012, Petzold-Maxwell et al. 2013b, Rudeen et al. 2013), although questions remain about commercial application of entomopathogens. Furthermore, *D. v. virgifera* has evolved resistance to several classes of insecticides, including organochlorines (Ball and Weekman 1962, 1963), carbamates (Meinke et al. 1998), organophosphates (Meinke et al. 1998) and pyrethroids (Pereira et al. 2015). Crop rotation has been used for *D. v. virgifera* management for over a century (Spencer et al. 2014), and is effective because *D. v. virgifera* larvae that hatch in fields rotated away from corn starve (Branson and Ortman 1970, 1971). However, rotation-resistant *D. v. virgifera* have adapted behaviorally crop rotation through a loss of host plant ovipositional fidelity (Levine et al. 2002, Gray et al. 2009).

***D. v. virgifera* & Bt Corn.** *Bacillus thuringiensis* (Bt) is a entomopathogenic, gram-positive soil bacterium that can be found ubiquitously throughout the environment

(Schnepfetal et al. 1998), and has been applied as a foliar insecticide for decades. During the stationary growth stage of Bt, it forms a parasporal crystal, and in this stage it can be characterized as an entomopathogen (Schnepfetal et al. 1998). Bt kills insects through a multi-step process; 1) the crystal form of Bt, containing the protoxin, is ingested by the insect host, 2) solubilization of crystal into the active toxin in the insect midgut, 3) proteolyic digestion of the active fragment 4) binding of the active toxin to the insect brush boarder membrane in the midgut and 5) insertion of the toxin into the apical membrane forming which destroys the midgut epitheal cells integrity causing the insect host to die of osmatic shock (Gould 1998, Schnepfetal et al. 1998).

In 1996, crops genetically modified to expressed toxins derived from Bt that target pest insects became commercially available in the U. S. (Gould 1998). Bt crops are effective pest management tools because they reduce the need for conventional insecticides, reduced impacts on beneficial insects and natural enemies of pest species and suppress of pest populations (Shelton et al. 2002, Mendelsohn et al. 2003, Cattaneo et al. 2006, Hellmich et al. 2008, Hutchison et al. 2010, Tabashnik et al. 2010). By 2015, 72% of corn planted in the U. S. expressed Bt toxins for insect management (USDA, NASS 2015). Bt corn targeting *D. v. virgifera* became commercially available in 2003 (EPA 2003). There are currently four commercially available Bt toxins that target *Diabrotica* spp., expressed in corn either singly or in pyramids; Cry3Bb1, Cry34/35Ab1, mCry3A and eCry3.1Ab (Cullen et al. 2013).

The high adoption rate of Bt crops increases the selection pressure on pests to evolve resistance. Several different strategies have been proposed to delay pest resistance to Bt crops. Gould (1998) outlines four different strategies: 1) the use of non-toxic refuges to sustain susceptible alleles in the pest population, 2) the use pyramids, 3) using low does

toxins coupled with natural enemies and 4) tissue, time, or injury specific expression of toxin. Gould (1998) also proposed a fifth strategy, though he doesn't label it as such, which was cultivars expressing a high dose of toxin.

In the U. S., registration of Bt crops is coupled with Insect Resistance Management (IRM) strategies to delay the development of Bt-resistant pest populations. The principle IRM plan for Bt crops is the refuge strategy, which uses non-Bt host plants (refuge) to sustain a source of susceptible individuals that mate with resistant individuals from Bt crops (Gould 1998). Refuges are most effective at delaying resistance when they are used in conjunction with high-dose Bt toxins or with Bt pyramids, resistance is inherited recessively and resistant alleles are initially rare (Tabashnik 1994, Gould 1998, Roush 1998, Tabashnik et al. 2004). Furthermore, high-dose Bt toxins kill 99.99% of susceptible individuals or produced at 25 times the concentration to kill a susceptible individual, making resistance functionally recessive. For single trait Bt crops, Bt resistance is delayed if heterozygous offspring have lower fitness on a Bt crop compared to their homozygous-resistant parent (Tabashnik et al. 2008). Resistance is delayed in pyramided Bt crops when the toxins in the pyramid have independent modes of action (i.e., each toxin kills individuals that have resistance alleles for the other toxin) and mortality is high for homozygous susceptible individuals (Comins 1986, Gould 1998, Tabashnik and Gould 2012).

There are several problems confronting the refuge strategy's goal to delay evolution of Bt resistance in *D. v. virgifera*. Firstly, none of the four Bt toxins presently available that targeting *D. v. virgifera* are high-dose events (Hibbard et al. 2011, Gassmann 2012). Models have shown that the rate of resistance evolution increases as the resistance allele frequency increase or resistance is not inherited recessively (Gould 1998, Tabashnik et al. 2004). For *D.*

v. virgifera, greenhouse experiments found that resistance is inherited non-recessively (Lefko et al. 2008, Meihls et al. 2008) while resistance allele frequency for Cry3Bb1 Bt toxin is estimated to be 2,000 times greater than estimates used to model *D. v. virgifera* evolution to Bt (Onstad and Meinke 2010, Tabashink and Gould 2012). Laboratory strains of *D. v. virgifera* have been selected for resistance to each of the four Bt toxins, and resistance is observed to develop as rapidly as three to eight generations (Lefko et al. 2008, Meihls et al. 2008, 2011; Frank et al. 2013, Deitloff et al. 2015).

Bt resistance in laboratory-selected *D. v. virgifera* strains remains even in the absence of selection pressure (Meihls et al. 2008), indicating that Bt resistance is likely to persist in *D. v. virgifera* populations. Fitness costs are often associated with Bt resistance, and there is a positive correlation between the magnitude of fitness costs and the resistance ratio (Gassmann et al. 2009). However, resistance ratios for Cry3Bb1-resistant *D. v. virgifera* are relatively low compared to other Bt-resistant pests (Gassmann et al. 2009), and fitness costs associated with Bt resistance in *D. v. virgifera* have been correspondingly minimal (Petzold-Maxwell et al. 2012, Hoffmann et al. 2014, Ingber and Gassmann 2015).

Even with an IRM plan in place, within seven years of the commercialization of Bt corn expressing Cry3Bb1, cornfields in Iowa were observed with severe root injury associated with field-evolved resistance to Cry3Bb1 by *D. v. virgifera* (Gassmann et al. 2011). More reports of Cry3Bb1 resistance in Iowa, Illinois and Nebraska were soon published (Gassmann et al. 2012, 2014; Gray 2014, Wangila et al. 2015), as well as cross-resistance between Cry3Bb1 and mCry3A toxins (Gassmann et al. 2014, Wangila et al. 2015). Fields from which Bt-resistant *D. v. virgifera* were initially sampled were characterized by continuous planting of corn and continuous planting of Cry3Bb1 corn

(Gassmann et al. 2011, 2012). At present, there are no reports of field-evolved resistance by *D. v. virgifera* to either Cry34/35Ab1 (Gassmann et al. 2014) or eCry3.1Ab.

Bt corn IRM has recently incorporated the use of pyramided corn with multiple Bt toxins targeting *D. v. virgifera* after the first pyramided Bt corn was registered in 2009. However, the effectiveness of pyramids to delay resistance is reduced if cross-resistance exists among toxins or mortality of susceptible individuals is reduced (Roush 1998). Pyramiding soil-applied insecticides with Bt corn is detrimental to Bt corn IRM over time because soil insecticide does not kill enough larvae to delay resistance to Bt corn (Petzold-Maxwell et al. 2013a). Furthermore, field experiments have demonstrated that combining soil applied insecticide with Bt corn delays adult emergence (Petzold-Maxwell et al. 2013a), which can promote assortative mating of Bt-selected individuals leading to more rapid Bt resistance evolution (Gould 1998).

Cross-resistance among Bt toxins has been document in several pest species. Cross-resistance was found in *Heliothis virescens* Fabricius (Lepidoptera: Noctuidae), Tobacco budworm, among Cry1Ac, Cry1Ab and Cry2A toxins (Gould et al. 1992, Jurat-Fuentes et al. 2003). *Pectinophora gossypiella* Saunders (Lepidoptera: Gelechiidae), pink bollworm, were found to have asymmetrical cross-resistance, where resistance to Cry2Ab confers some resistance to Cry1Ac, but Cry1Ac does not confer any resistance to Cry2Ab (Tabashnik et al. 2009). Cross-resistance between Cry3Bb1 and mCry3A toxins by *D. v. virgifera* been documented (Gassmann et al. 2014, Wangila et al. 2015), and worryingly, there are no Bt pyramids available for *Diabrotica* spp. management that do not express either Cry3Bb1 or mCry3A toxin (Cullen et al. 2013). There is no evidence of cross-resistance between either Cry3Bb1 or mCry3A with Cry34/35Ab1 (Gassmann et al. 2011, 2012, 2014), however,

cross-resistance among the three Cry3 toxins (Cry3Bb1, mCry3A and eCry3.1Ab) is probable due to the structural similarity of these toxins (Carriere et al. 2015).

Integrated Pest Management (IPM) combines multiple management strategies (i.e., Bt corn, conventional insecticides, crop rotation, scouting) with knowledge of pest ecology to sustainably manage pest populations (Stern et al. 1959). IPM can facilitate IRM by diversifying the cause of pest morality and reducing the selection pressure for each source of mortality (McGaughey and Whalon 1992). Incorporating alternate *D. v. virgifera* management tactics, such as crop rotation or conventional insecticides, in addition to judicious use of Bt crops may mitigate the risk of injury from Cry3Bb1 and mCry3A-resistant *D. v. virgifera* and sustain the efficacy of the remaining Bt toxins (Gassmann 2012, Tabashnik and Gould 2012).

***Diabrotica barberi*.** *Diabrotica barberi* Smith & Lawrence (Coleoptera: Chrysomelidae), northern corn rootworm, is another major of corn in North America. *Diabrotica barberi* are univoltine and corn is the primary host plant. Adult *D. barberi* primarily consume corn pollen, silks and kernels, but they readily forage for pollen from other plants (Levine and Oloumi-Sadeghi 1991, Spencer et al. 2009). Eggs are oviposited exclusively in the soil of cornfields and diapause through the winter. Larvae hatch during spring, feed on corn roots, pupate near the soil surface and emerge as adults typically during June. Similarly to *D. v. virgifera*, *D. barberi* larvae feeding injury can inhibit water and nutrient uptake and reduces the capacity of the root to hold the plant upright (Levine and Oloumi-Sadeghi 1991, Spencer et al. 2009).

Management of *D. barberi*. *Diabrotica barberi* are not as adept at overcoming pest management practices as *D. v. virgifera*, and are susceptible to soil and foliar-applied

insecticides (Ball and Weekman 1962, 1963; Spencer et al. 2014). Bt corn targeting *D. v. virgifera* also targets *D. barberi,* but to date there have been no documented cases of Bt resistance by *D. barberi*. However, *D. barberi* have been observed to successfully emerge as adults from Bt corn (Petzold-Maxwell et al. 2013b, Keweshan et al. 2015).

Both *D. v. virgifera* and *D. barberi* have evolved resistance to crop rotation, although the resistance mechanisms differ between the species (Spencer et al. 2014). Injury to first-year corn by *D. barberi* was first recorded in the 1920's (Bigger 1932). While *D. v. virgifera* evolved a behavioral adaption to crop rotation, *D. barberi* circumvent crop rotation with a physiological adaptation of variable length, extended diapause (Krysan et al. 1984, Levine et al. 1992). Oviposition by *D. barberi* still occurs exclusively in cornfields; however, up to 40% of eggs will hatch after two winters (Krysan et al. 1984). Furthermore, diapause has been observed to extend between one and four years in length and the proportion of that egg hatch each year can adapt to field-specific cropping practices (Levine et al. 1992).

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CHAPTER 2.

IMPACTS OF RYE COVER CROP ON BENEFICIAL ARTHROPODS

A paper submitted to *Environmental Entomology*

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Abstract

Increased vegetational diversity within cropping systems can positively affect natural enemy communities. Cover crops are beneficial to agroecosystems because they decrease soil erosion and increase soil health. Additionally, cover crops increase within field vegetational diversity. We hypothesized that a rye cover crop planted within rotated corn and soybean would positively affect the epigeal and canopy, beneficial arthropod communities compared to rotated corn and soybean grown without a cover crop. From 2011 through 2013, arthropod communities were measured at two locations in Iowa using pitfall traps and sweep nets throughout the growing season. Captured arthropods were identified to order and family level taxonomic units, and assigned to functional groups. Most taxa did not significantly respond to the presence of the rye cover crop when analyzed individually. When taxa were analyzed as groups, activity-density of epigeal predators in soybean was significantly greater in plots with the rye cover crop. The rye cover crop did not affect epigeal predators captured in corn and foliar predators and parasitoids in soybean. Activity-density of non-predators, including granivores and detritivores, also were unaffected by the presence of the rye cover crop. Gryllidae was the only taxa that had significantly greater activity-density in plots without a rye cover crop. These data partly agree with the enemies hypothesis, which posits that

increased diversity within fields supports a greater abundance of natural enemies. However, as pest abundance was not measured in this study, the extent to which differences in predator activity-density observed here could reduce pest pressure remains untested.

Introduction

Ecosystem services provided by arthropods include biological control of agricultural pests (Losey and Vaughan 2006). There is evidence that agroecosystems with greater vegetational diversity, compared to monocultures, can lead to decreased pest abundance and increased natural enemies abundance (Andow 1991a, Landis et al. 2000). Vegetational diversity can vary temporally, from crops that completely overlap in time (i.e., intercropping) to crops that are completely separated in time (i.e., traditional crop rotation schemes). Spatial diversity in agroecosystems can change at the landscape level or within fields, and even within plants. Reviews of studies that manipulated within field diversity have shown that when diversity is increased there are positive effects on natural enemy abundance and negative effects on insect pest abundance (Langellotto and Denno 2004, Letourneau et al. 2011). There are many hypotheses that explain why agroecosystems with greater diversity can reduce pest abundance. The resource concentration hypothesis predicts that pests with narrow host ranges have lower recruitment and retention in polycultures compared to monocultures (Root 1973). The host-quality hypothesis predicts that pest abundance is reduced in polycultures because competition among crop species, and among crop and non-crop species, lowers host-plant quality (Bach 1981, Bukovinszky et al. 2004). The enemies hypothesis proposes that pest populations are reduced in diverse agroecosystems because natural enemies are more abundant (Root 1973).

The addition of a cover crop increases vegetational diversity within fields (Andow 1991b). Cover crops are non-crop species planted prior to or intercropped with a cash crop (Andow 1991b, Hartwig and Ammon 2002). The benefits of adding a cover crop include reducing soil and nutrient loss, improving soil health, and suppressing weeds (USDA, NRCS 2013). Rye (*Secale cereale* L.) has been recommended as a cover crop in the U.S. Corn Belt because of its cold tolerance and rapid growth early in the spring (Stoskopf 1985, Bollero and Bullock 1994, Dinnes et al. 2002). A rye cover crop in the Corn Belt is typically seeded in the fall and terminated in the spring before the cash crop is planted (Clark 2007, Casey 2012).

Cover crops may decrease insect pest abundance by creating habitat for natural enemies (Carmona and Landis 1999, Landis et al. 2000). Vegetation within fields can affect natural enemies by altering their mobility, the abundance of alternate prey or hosts, and the availability of favorable microclimates (Sunderland and Samu 2000, Symondson et al. 2002). European corn borer (*Ostrinia nubilalis* Hubner [Lepidoptera: Crambidae]) used as sentinel prey in corn (*Zea mays* L.) and soybean (*Gylcine max* L.) plots were consumed at greater frequency in plots planted with an alfalfa (*Medicago sativa* L.) and kura clover (*Trifolium ambiguum* M. Bieb.) living-mulch cover crop (a type of cover crop that is grown concurrently with a cash crop) than without a cover crop (Prasifka et al. 2006). Foliar predators in soybean plots were both significantly more abundant and diverse in soybean canopies when plots also included a living-mulch cover crop of alfalfa (Schmidt et al. 2007). Furthermore, soybean aphid (*Aphis glycines* Matsumura [Hempitera: Aphididae]) population growth rates were lower in soybean plots with the living-mulch cover crop. Reduction in pest insect abundances also have been observed when rye was included as a cover crop, however

the effect of rye on natural enemy abundance has been inconsistent (Bottenberg et al. 1997, Tillman et al. 2004, Koch et al. 2012). Furthermore, rye cover crop management can alter the responses of both pests and natural enemies (Smith et al. 1988, Laub and Luna 1991, 1992).

The goals of this study were to quantify the effects of a rye cover crop planted within annually rotated corn and soybean on the composition and abundance of both epigeal and canopy beneficial arthropods. We hypothesized that the presence of a rye cover crop in this annual rotation would have a positive effect on the beneficial arthropod community and individual taxa. To test this hypothesis, pitfall traps and sweep nets were used over a three-year period to measure beneficial arthropod communities found within plots of annually rotated corn and soybean grown with and without a rye cover crop.

Material and Methods

Experimental Design and Field Sites. Data were collected at two locations per year during 2011, 2012, and 2013 in Iowa; the Agricultural Drainage Water Research Site (ADW; Gilmore City, Pocahontas County, Iowa) and the Iowa State University Agronomy and Agricultural Engineering Research Farm (ISUAG, Boone, Boone County, Iowa). Both ADW and ISUAG have grown corn and soybean in a rotation since the 1900's (Daigh et al. 2014). At each location, no-tillage corn and soybean were rotated annually in replicated plots of 15 m × 38 m and 15 m × 6 m for ADW and ISUAG, respectively. Beginning in 2008 at ISUAG and 2010 at ADW, a rye cover crop was added into the corn-soybean rotation (Daigh et al. 2014). Rye seed was drilled (100 and 63 kg ha^{-1} for ADW and ISUAG, respectively) into a subset of randomly selected plots in the fall following the harvest of the cash crop. Rye was terminated in the spring approximately two weeks before planting of either corn or soybean using herbicide (glyphosate). At each location, both corn and soybean were grown with and

without a cover crop, with each combination replicated twice in a randomized complete block design.

Arthropod Sampling. During each year and at both locations, four plots of corn and soybean grown with and without a rye cover crop were sampled, for a total of 16 plots per location. Each plot was sampled for epigeal and canopy beneficial arthropods. In 2011, ADW was sampled on 21 June, 19 July, 4 August, and 4 September and ISUAG was sampled on 29 June, 19 July, 5 August, and 4 September. During 2012, both locations were sampled on the same days; 25 June, 16 July, 6 August, and 1 September. Similarly, during 2013, both locations were sampled on the same days; 20 June, 15 July, 9 August, and 7 September.

Pitfall traps were used to estimate the activity-density of epigeal arthropods. Three pitfall traps were placed within each plot, and consisted of 1 L cups (Reynolds Food Packaging, Shepherdsville, Kentucky) buried in the ground flush with the soil surface. A cover, raised ca. 5 cm above the soil surface, was used to prevent debris from entering pitfall traps (Hummel et al. 2012). To prevent arthropods from escaping traps, the bottom of each pitfall container was filled with ca. 100 mL of non-scented, soapy water solution. Pitfall traps remained in plots for 24 h during each sampling period. After 24 h, contents of pitfall traps were placed separately into sealable plastic bags and stored in freezers until contents were sorted.

Sweep nets were used to sample beneficial arthropods in soybean canopies. A sample consisted of 15 continuous pendulum sweeps of the upper soybean canopy. Sweeping locations within plots were arbitrarily chosen, but never at a plot edges. One sweep net sample was collected per plot. Sweep net sample contents were separately placed in sealable plastic bags and stored in freezers until contents were sortied.

Insects captured in pitfall traps were identified to family, and non-insect arthropods were identified to class, order, or family depending upon the taxa. Taxa from pitfall traps were further sorted into two groups, predators and non-predators. Taxonomic groups do not always fit perfectly into these two functional groups. Carabidae (Coleoptera) were classified here as predators (Duelli et al. 1999), though many species within this family can be considered omnivores that feed on both arthropods and weed seeds (Kromp 1999, O'Rourke et al. 2006; Pullaro et al. 2006, Westerman et al. 2008). Taxa classified as non-predators included granivores and detritivores. Formicidae (Hymenoptera) were classified as non-predators as they are generally considered weed seed predators (Inouye et al. 1980, Baraibar et al. 2009), though Formicidae has also been described as a predator (Dively and Rose 2003) and as a detritivore (Bhatti et al. 2005). Gryllidae (Orthoptera) were grouped as non-predators because they are primarily described as granivores (Carmona et al. 1999, Westerman et al. 2008). Insects captured by sweeps nets were identified to family or superfamily, and non-insect arthropods were identified to order. Beneficial taxa collected by sweep nets were sorted into two groups, predators and parasitoids.

Statistical Analysis. For all analyses, pitfall trap and sweep net data were analyzed separately. Furthermore, pitfall trap data were analyzed separately by crop. Taxa were only included in analyses if they composed > 5% of total number of individuals captured (Costamagna and Landis 2004). Nonmetric multidimensional scaling (NMDS), multivariate analysis of variance (MANOVA) and analysis of variance (ANOVA) were used to compare differences in beneficial arthropod community composition and to compare individual taxa by cover treatment (rye cover crop present or absent), sampling date, and their interaction.

To compare the composition of beneficial arthropod communities, NMDS analyses using Sorensen (Bray-Curtis) distances (Krebs 1999) were performed in R 3.1 statistical software (Dixon 2003, Oksanen 2013, R Core Team 2014). The NMDS summarizes the relationships among all variables and displays the relationships in ordination space. The composition of beneficial arthropod communities, represented by points within the ordination, becomes increasingly similar in composition as distances among points within the NMDS decreases. Function metaMDS in R was used to create NMDS ordination plots. Stress (S) and ordination non-metric fit (r^2), statistics measuring goodness of fit between the ordination distances and the data dissimilarity, were also computed (Oksanen 2013). The function envit in R was used to create centroids of mean community composition and vectors describing changes in taxa activity-density or abundance (Oksanen 2013). Centroids created represented the mean community composition for each cover treatment by sampling date combination. The vector direction within an ordination indicates the direction of most rapid increase of a taxa's activity-density or abundance. The significance of each vector's relationship to the ordination were calculated from 999 random permutations of these data (Oksanen 2013). Vectors were displayed only if they had a significant relationship with the ordination.

Activity-density of taxa were analyzed with repeated-measures MANOVA, based on a split-plot design (Quinn and Keough 2002), that included the factors of cover treatment, sampling date and their interaction in SAS statistical software version 9.3 (PROC GLM) (SAS Institute, Cary, North Carolina). Data were log (x + 0.5) function transformed to increase the normality of the residuals. Fixed model effects were cover treatment, sampling date and the interaction of cover treatment and sampling date. Random effects included year,

location, the interaction of year and location, plot nested within the interaction of year × location × cover treatment and sampling date × plot nested within year × location × cover treatment. The inclusion of the sampling date × plot nested within year × location × cover treatment term in the model makes this a repeated-measures design.

Total capture, capture by group and capture of each individual taxa were analyzed using repeated measures ANOVA (PROC MIXED) in SAS 9.3. Total captured was measured as the activity-density or abundance of all individuals captured by pitfall traps or sweep nets. Capture by group was measured as the activity-density or abundance of all individuals assigned to a specific group. To meet the assumptions of the ANOVA, data were transformed by the log (x + 0.5) function. Cover treatment, sampling date, and their interactions were classified as fixed effects. Random effects were year, location, the interaction of year and location, plot nested within the interaction of year × location × cover treatment and sampling date × plot nested within year × location × cover treatment. When significant effects were present, pairwise comparisons were made using the PDIFF option (in PROC MIXED). Alpha levels were adjusted for multiple comparisons using the Bonferroni correction.

Results

Pitfall traps in corn plots captured over 2,200 individual beneficial arthropod, representing nine different taxa. Six of those taxa individually represented > 5% of the total community and were included in all analyses (Table 1). Epigeal taxa from corn plots excluded were Isopoda, Chilopoda, and Staphylinidae (Coleoptera). More than 2,500 beneficial arthropods representing nine different taxa were captured by pitfall traps in soybeans plots, and five taxa each composing > 5% of the total capture were included in analyses (Table 1). Excluded taxa included Isopoda, Chilopoda, Opiliones (Arachnida), and

Staphylinidae (Coleoptera). Thirteen different beneficial taxa were captured by sweep net sampling of soybean canopies. Eight taxa were captured in abundances > 5% of the total number of individuals captured (Table 1). The remaining taxa that were excluded from sweep net community analyses were Reduviidae (Hemiptera), Braconidae (Hymenoptera), and Ichneumonidae (Hymenoptera), Asilidae (Diptera), and Dolichopodidae (Diptera).

Analysis by NMDS reached solutions with low stress for pitfall trap data from corn (S = 0.09; Fig. 1A), pitfall trap data from soybean (S = 0.07; Fig. 2A) and sweep net data from soybeans (S = 0.11; Fig. 3A). Additionally, NMDS ordination distances correlated with corn and soybean pitfall trap and soybean sweep net data dissimilarity (non-metric fit r^2 = 0.992, 0.995, and 0.988, respectively). The rye cover crop did not significantly affect total beneficial arthropod composition in any of the three communities sampled as tested by MANOVA (Table 2). However, epigeal and canopy community compositions from both corn and soybean were significantly affected by sampling date (Table 2). Furthermore, there was a marginally significant cover treatment by sampling date effect on beneficial taxa composition as captured by pitfall traps from soybean plots (Table 2).

Predator taxa captured from pitfall traps in soybean plots was the only group significantly affected by the presence of the rye cover crop (Table 3). Activity-density of predators was significantly greater in soybean plots that included a rye cover crop (rye: 5.2 ± 2.3; no cover: 3.3 ± 1.5 [mean activity-density / plot ± SEM]). Overall epigeal activity-density and non-predator taxa activity-density did not differ by cover treatment in either corn or soybean plots (Table 3). However, the activity-density of epigeal predator taxa from corn and soybean plots and non-predators from corn plots significantly differed by sampling date (Table 3). Epigeal predator activity-density in both corn (Fig. 1B) soybean (Fig. 2B) were

significantly greater during June and July sampling compared to sampling later in the year. Activity-density of non-predators from corn plots was significantly greater when sampled during September (Fig. 1B). Analysis of overall epigeal activity-density in soybean plots showed that sampling date did have a significant effect (Table 3), however there were no significant pairwise comparisons among sampling dates after adjusting alpha levels for multiple comparisons. In soybean canopies, total beneficial abundance and predator abundance were both significantly affected by sampling date (Table 3). Total beneficial and predator abundance as capture by sweep netting was the lowest during June and then increased significantly during July, August and September (Fig. 3B). Parasitoid abundance in soybean canopies was not affected by sampling date (Table 3; Fig. 3B).

When taxa were analyzed individually by ANOVA, Carabidae and Gryllidae captured from soybean plots were the only taxa significantly affected by the cover treatment (Table 4; Supp. Table S1). Activity-density of Carabidae was significantly greater in soybean plots that included the rye cover crop. Gryllidae responded conversely; activity-density was significantly greater in soybean plots without a cover crop. The majority of taxa were affected by sampling date, with Syrphidae and Tachinidae captured from soybean canopies the only two exceptions (Table 4; Supp. Table S1). In both corn and soybean pitfall traps, Lycosidae, Carabidae, and Formicidae each had greater activity-density when sampled earlier in the year. Opiliones and Gryllidae had greater activity-densities when sampling occurred later in the year. Diplopoda were captured significantly more often during the beginning and end of each season, and were rarely captured during July and August sampling. In soybean canopies, Anthocoridae, Nabidae, Chrysopidae, Coccinellidae, Chalcidoidea were all less abundant during June and then abundances tended to increase as the season progressed.

Araneae were captured in greatest abundance from soybean canopies in the middle of season, during July and August sampling.

Vectors describing changes in activity-density or abundance of individual taxa were significantly correlated to the NMDS ordinations for the majority of taxa, with the exceptions of Diplopoda captured from both corn and soybean pitfall traps and Chalcidoidea collected from soybean canopies (Table 5). Within epigeal communities of both crops, changes in Formicidae and Gryllidae activity-density were best represented by the NMDS ordinations (Table 5; Figs. 1A and 2A). In soybean canopies, dissimilarity within the NMDS best described the changes in Coccinellidae abundance (Table 5; Fig. 3A).

Discussion

The objective of this study was to quantify the effects of a rye cover crop planted within annually rotated corn and soybean on both the epigeal and canopy, beneficial arthropod communities. Only modest differences were observed in the composition and abundance of beneficial arthropods between either corn or soybean grown with or without a rye cover crop. Most taxa did not respond significantly to the presence of the rye cover crop when analyzed individually (Table 4). However, when taxa were analyzed as groups, epigeal predators in soybean plots responded positively to the presence of the rye cover crop (Table 3). Community compositions were more often affected by sampling date (Table 2), as capture of nearly all individual taxa significantly varied by sampling date (Table 4; Supp. Table S1).

The enemies hypothesis predicts that natural enemies such as predators and parasitoids would be more abundant in agroecosystems with greater vegetational diversity compared to monocultures (Root 1973, Andow 1991a). Our data partially support the

enemies hypothesis as epigeal predators in soybean responded significantly and positively to the increased diversity within plots that included the rye cover crop (Table 3; Fig. 2B). Carabidae captured from soybean plots were the only individual taxa in the entire study to have significantly greater activity-density when rye was present, though this occurred only in plots when rye was planted before soybeans (Table 4). Carabidae are a diverse group with a wide range of life-history traits (Kromp 1999), and Carabidae response to field-level management can vary by practice, such as tillage (Brust et al. 1986, Menalled et al. 2006) or organic farming (Garratt et al. 2011). For example, Menalled et al. (2006) found significantly more Carabidae in conventionally tilled plots compared no till plots, yet the percentage of weed-seed predator species increased from 4% of individuals in the conventionally tilled plots to 32% of individuals in the no tillage plots. Activity-density of Lycosidae in both corn and soybean plots were numerically greater in the rye cover crop treatment, though the differences were not significant (Table 4). This results was surprising because Araneae have been observed to respond strongly to increased diversification within fields (Sunderland and Samu 2000, Langellotto and Denno 2004).

Natural enemies in soybean canopies primarily consist of predators (Rutledge et al. 2004, Schmidt et al. 2008), and predators represented three quarters of beneficial taxa captured from soybean canopies with sweep nets (Table 1). Though foliar predators in soybean do respond positively to some living-mulch cover crops (Schmidt et al. 2007), we observed no effect of a rye cover crop on predator abundance in soybean canopies (Table 3; Fig. 3B). Other studies have reported similar results. Organic soybean fields in Minnesota planted with and without a rye cover crop did not differ in foliar predator abundance (Koch et al. 2012). The addition of a rye cover crop into snap beans (*Phaseolus vulgaris* L.) also had

no effect on foliar predators, and when rye was combined with another cover crop, red clover (*Trifolium pretense* L.), abundance of the predacious insidious flower bug (*Orius insidiosus* Say [Hempitera: Anthocoridae]) was reduced (Bottenberg et al. 1997). Foliar predator abundance in soybean was affected by sampling date (Table 3). The abundance of predator taxa in soybean plots increased as the season progressed (Fig. 3B), which is consistent with other studies that have sampled predators from soybean canopies in Iowa (Schmidt et al. 2008). Parasitoids represented a quarter of all beneficial arthropods captured from soybean canopies (Table 1). We anticipated that parasitoid abundance would increase in fields with greater vegetational diversity, as predicted by the enemies hypothesis, and in some studies, greater habitat complexity has been shown to positively affect parasitoid abundance (Langellotto and Denno 2004). However, we found no evidence that the rye cover crop increased parasitoid abundance, because parasitoids as a group and individually did not differ between plots with or without the rye cover crop (Tables 3 and 4).

Total beneficial arthropod composition of all three sampled communities were affected by sampling date but not by the presence of the rye cover crop, however, there was a marginally significant interaction of sampling date and cover treatment on epigeal community composition in soybean plots (Table 2). The soybean epigeal community NMDS helps to visualize the interaction of these two effects (Fig. 2A). Ordination axes in NMDS are unitless, however there does appear to be some relationship between NMDS axis 2 and cover treatment. Soybean plots with the rye cover crop had numerically greater activity-density of beneficial arthropods during June, July, and August compared to plots without the cover crop. During September sampling, this trend reversed and plots without the rye cover crop captured twice as many beneficial arthropods as soybean plots with the rye cover crop.

Comparing centroids within each sampling date, the rye cover crop treatment centroids are always lower on the NMDS 2 axis compared to their respective no cover crop treatment centroids (Fig. 2A). Epigeal predators in soybean plots were captured more frequently from plots that had the rye cover crop, which matches the downward moving vectors of both predator taxa (Lycosidae and Carabidae). Gryllidae had significantly greater activity-density in soybean plots without the rye cover crop (Table 4), and its activity-density vector move upwards within the ordination (Fig. 2B). Additionally, Carabidae were more frequently captured during June and July sampling dates, while Gryllidae were least frequently captured during June sampling (Table 4). Similar temporal patterns have been observed in other studies conducted in the Corn Belt for both Carabidae (O'Rourke et al. 2008) and Gryllidae (Carmona et al. 1999).

How rye cover crop is managed within fields could further complicated predator and pest interactions. The recommended time that a rye cover crop should be terminated is two to three weeks before the cash crop is planted in order to prevent the rye from negatively affecting the cash crop (Tollenaar et al. 1993, Casey 2012, MCCC 2012). Rye termination can be achieved by mechanical processes (i.e., mowing, crimping, or tillage) or terminated chemically with herbicide (Clark 2007, Casey 2012). A study measuring the effect of rye termination practices on parasitoid and predator activity in corn found that early-season activity-densities of Lycosidae and Carabidae peaked earlier in the year when rye was destroyed by mowing compared to destruction with an herbicide (Laub and Luna 1992). From the same experiment, however, parasitoid rates did not differ between rye cover crop destruction practices. Soybean insect pests also respond variably to different rye cover crop termination methods (Smith et al. 1988). Potato leafhopper (*Empoasca fabae* [Hemiptera:

Cicadellidae]) was found in greater abundance in soybeans plots that either did not have a rye cover crop or had a rye cover crop that was incorporated into the soil with disk tillage. Conversely, Japanese beetle (*Popillia japonica* [Coleoptera: Scarabaeidae]) and bean leaf beetle (*Cerotoma trifurcata* [Coleoptera: Chrysomelidae]) were significantly more abundance in soybeans plots where the rye cover crop was terminated with herbicide and left standing.

Activity-density of Gryllidae in soybean plots was significantly reduced in the rye cover crop treatment (Table 4), though capture of non-predators as a group was not affect by the presence of the rye cover crop in either corn or soybean plots (Table 3). Granivores, including Gryllidae and Formicidae, significantly contribute to weed suppression (Menalled et al. 2006, Westerman et al. 2008, Baraibar et al. 2009), and cover crops can positively affect the activity-density of weed seed predators (Ward et al. 2011). Why Gryllidae was captured more frequently in plots without the rye cover crop is unclear. One hypothesis could be that suppression of weeds over time by the rye cover crop may have decreased the availability of food resources for granivores. The growth of weed seedbanks are positively related to weed biomass (Teasdale et al. 2003), and the addition of a rye cover crop has been shown to both reduce weed biomass (Moyer et al. 2000, Weston and Duke 2003) and weed seedbank density (Moonen and Barberi 2004). However, neither the weed biomass nor weed seedbank density were measured during this study.

Cover crops can benefit corn and soybean farmers by reducing the loss of soil and nutrients (Hartwig and Ammon 2002) and suppressing weed and insect pests (Weston and Duke 2003, Koch et al. 2012). The results of this study suggest that adding a rye cover crop to annual rotations of corn and soybean can positively affect some epigeal predators in the

soybean phase of the rotation. These data partly support the enemies hypothesis that greater vegetational diversity within fields will increase abundance of natural enemies (Root 1973), as predator taxa collected from the soil surface were more abundant in plots that included the rye cover crop. The enemies hypothesis also predicts that the greater presence of natural enemies in diverse cropping systems would result in decreased pest pressure. As pest abundance was not measured in this study, the extent that the differences in predator activity-density observed here would reduce pest pressure remains untested.

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Tables

Table 1. Taxa captured from corn and soybean plots by sampling method

Sample Method				Total Capture (%)	
Class	**Order**	**Family**	**Group**	**Corn**	**Soybean**
Pitfall trap				2,215 (100%)	2,564 (100%)
Diplopoda			Non-predator	261 (12%)	121 (5%)
Arachnida	Opiliones		Predator	103 (5%)	.
	Araneae	Lycosidae	Predator	248 (11%)	558 (22%)
Insecta	Coleoptera	Carabidae	Predator	163 (7%)	247 (10%)
	Hymenoptera	Formicidae	Non-predator	415 (19%)	812 (32%)
	Orthoptera	Gryllidae	Non-predator	1,025 (46%)	826 (32%)
Sweep net				.	481 (100%)
Arachnida	Araneae		Predator	.	61 (13%)
Insecta	Hemiptera	Anthocoridae	Predator	.	48 (10%)
		Nabidae	Predator	.	30 (6%)
	Neuroptera	Chrysopidae	Predator	.	90 (19%)
	Coleoptera	Coccinellidae	Predator	.	85 (18%)
	Hymenoptera	Chalcidoidea	Parasitoid	.	48 (10%)
	Diptera	Syrphidae	Predator	.	62 (13%)
		Tachinidae	Parasitoid	.	57 (12%)

Table 2. Multivariate analysis of variance of total beneficial arthropods captured from corn and soybean plots by sampling method and crop

Sampling Method	**Cover Treatment**			**Sampling Date**			**Trt*Date**		
Crop	***F***	**df**	***P***	***F***	**df**	***P***	***F***	**df**	***P***
Pitfall trap									
Corn	0.21	1, 40	0.65	4.36	3, 135	**0.006**	1.98	3, 135	0.12
Soybean	0.27	1, 41	0.60	6.05	3, 136	**0.0007**	2.40	3, 136	0.07
Sweep net									
Soybean	0.04	1, 41	0.84	8.24	3, 137	**<0.0001**	1.29	3, 137	0.28

Table 3. Analysis of variance of total beneficial and groups of arthropods captured from corn and soybean plots by sampling method and crop

Sampling Method / Crop	**Cover Treatment**			**Sampling Date**			**Trt*Date**		
Group	***F***	**df**	***P***	***F***	**df**	***P***	***F***	**df**	***P***
Pitfall / Corn									
All Beneficials	0.65	1, 40	0.41	2.16	3, 135	0.10	1.83	3, 135	0.14
Predators	0.01	1, 40	0.96	7.76	3, 135	**<0.0001**	1.06	3, 135	0.37
Non-Predators	0.25	1, 40	0.62	3.45	3, 135	**0.019**	1.39	3, 135	0.25
Pitfall / Soybean									
All Beneficials	0.01	1, 41	0.99	2.79	3, 136	**0.043**[a]	1.56	3, 136	0.20
Predators	7.03	1, 41	**0.011**	10.12	3, 136	**<0.0001**	1.73	3, 136	0.16
Non-Predators	0.89	1, 41	0.35	1.18	3, 136	0.32	0.93	3, 136	0.43
Sweep net / Soybean									
All Beneficials	0.22	1, 41	0.64	10.08	3, 137	**<0.0001**	1.67	3, 137	0.18
Predators	0.01	1, 41	0.99	12.97	3, 137	**<0.0001**	1.34	3, 137	0.26
Parasitoids	0.37	1, 41	0.54	1.99	3, 137	0.12	1.47	3, 137	0.23

[a] No significant differences detected among sampling dates after adjusting alpha levels for multiple comparisons.

Table 4. Individual taxa captured per plot (mean ± standard error of the mean) from corn and soybean plots by sampling method and crop

Sampling Method/ Crop	Group/ Taxa	Cover Treatment[a]		Sampling Date[b]			
		No Cover :	Rye Cover	June	July	August	September
Pitfall trap / Corn	Predators						
	Opiliones	0.58 ± 0.15 :	0.51 ± 0.12	0.17 ± 0.08a	0.26 ± 0.08a	0.53 ± 0.16ab	1.23 ± 0.31b
	Lycosidae	1.13 ± 0.30 :	1.53 ± 0.61	1.53 ± 0.33a	2.96 ± 1.26a	0.30 ± 0.09b	0.49 ± 0.13b
	Carabidae	0.73 ± 0.14 :	1.01 ± 0.17	1.49 ± 0.33a	0.89 ± 0.17a	0.68 ± 0.16ab	0.40 ± 0.15b
	Non-Predators						
	Gryllidae	5.97 ± 0.75 :	4.91 ± 0.72	2.34 ± 0.43a	5.79 ± 0.86b	5.72 ± 0.96b	7.96 ± 1.47b
	Formicidae	1.84 ± 0.50 :	2.59 ± 0.94	4.91 ± 1.73a	2.21 ± 0.60ab	1.45 ± 0.92bc	0.26 ± 0.13c
	Diplopoda	2.02 ± 0.98 :	0.73 ± 0.18	0.98 ± 0.28a	0.00 ± 0.00b	0.00 ± 0.00b	4.57 ± 1.95c
Pitfall trap / Soybean	Predators						
	Lycosidae	3.23 ± 1.44 :	3.54 ± 2.32	1.63 ± 0.36a	8.81 ± 5.36a	0.40 ± 0.12bc	0.81 ± 0.17ac
	Carabidae	0.97 ± 0.18 :	1.63 ± 0.26*	2.02 ± 0.41a	1.19 ± 0.22ab	1.19 ± 0.34bc	0.79 ± 0.26c
	Non-Predators						
	Gryllidae	5.05 ± 0.69 :	3.66 ± 0.50*	1.02 ± 0.18a	6.54 ± 1.13b	4.32 ± 0.57b	5.53 ± 0.98b
	Formicidae	4.29 ± 1.71 :	4.26 ± 1.64	12.31 ± 4.26a	1.92 ± 0.45b	1.96 ± 1.29bc	0.79 ± 0.64c
	Diplopoda	0.69 ± 0.19 :	0.58 ± 0.16	0.79 ± 0.25b	0.06 ± 0.05c	0.02 ± 0.02c	1.68 ± 0.39a

[a] Significant difference in activity-density between cover treatments, denoted with '*'.

[b] Letters denotes significant differences in activity-density among sampling dates.

Table 4 Continued. Individual taxa captured per plot (mean ± standard error of the mean) from corn and soybean plots by sampling method and crop

Sampling Method/ Crop	Group/ Taxa	Cover Treatment[a]		Sampling Date[b]			
		No Cover :	Rye Cover	June	July	August	September
Sweep net / Soybean	Predators						
	Araneae	0.38 ± 0.08 :	0.26 ± 0.07	0.17 ± 0.07a	0.64 ± 0.16bc	0.29 ± 0.09ac	0.19 ± 0.08a
	Anthocoridae	0.20 ± 0.07 :	0.31 ± 0.13	0.00 ± 0.00a	0.26 ± 0.09ab	0.23 ± 0.09a	0.52 ± 0.25b
	Nabidae	0.13 ± 0.05 :	0.19 ± 0.05	0.02 ± 0.02a	0.13 ± 0.07a	0.08 ± 0.05a	0.04 ± 0.10b
	Chrysopidae	0.44 ± 0.12 :	0.51 ± 0.11	0.00 ± 0.00a	0.38 ± 0.15ab	0.73 ± 0.20b	0.77 ± 0.19b
	Coccinellidae	0.35 ± 0.15 :	0.54 ± 0.22	0.06 ± 0.05a	0.09 ± 0.05a	0.29 ± 0.11ab	0.13 ± 0.50b
	Syrphidae	0.42 ± 0.12 :	0.23 ± 0.08	0.21 ± 0.14	0.30 ± 0.12	0.54 ± 0.20	0.25 ± 0.09
	Parasitoids						
	Chalcidoidea	0.26 ± 0.07 :	0.24 ± 0.07	0.06 ± 0.04a	0.45 ± 0.11b	0.21 ± 0.10ab	0.29 ± 0.12ab
	Tachinidae	0.23 ± 0.07 :	0.37 ± 0.14	0.25 ± 0.08	0.21 ± 0.09	0.63 ± 0.28	0.10 ± 0.04

[a] Significant difference in activity-density between cover treatments, denoted with '*'.

[b] Letters denotes significant differences in activity-density among sampling dates.

Table 5. Vector coefficient of determinations for individual taxa within NMDS ordinations

Sampling Method		**Vectors**[a]			
Taxa	**Group**	r^2	***P***	r^2	***P***
Pitfall trap		**Corn**		**Soybean**	
Opiliones	Predator	0.10	0.001	.	.
Lycosidae	Predator	0.08	0.003	0.20	0.001
Carabidae	Predator	0.27	0.001	0.07	0.001
Formicidae	Non-Predator	0.64	0.001	0.56	0.001
Gryllidae	Non-Predator	0.59	0.001	0.46	0.001
Diplopoda	Non-Predator	0.02	0.24[b]	0.03	0.07
Sweep net		**Soybean**			
Araneae	Predator	0.29	0.001		
Anthocoridae	Predator	0.35	0.001		
Nabidae	Predator	0.08	0.003		
Chrysopidae	Predator	0.20	0.001		
Coccinellidae	Predator	0.71	0.001		
Syrphidae	Predator	0.36	0.001		
Chalcidoidea	Parasitoid	0.04	0.051		
Tachinidae	Parasitoid	0.14	0.006		

[a] Vector statistical significance based on 999 random permutations of the data

[b] Non-significant vectors are not displayed in NMDS figures

Figures

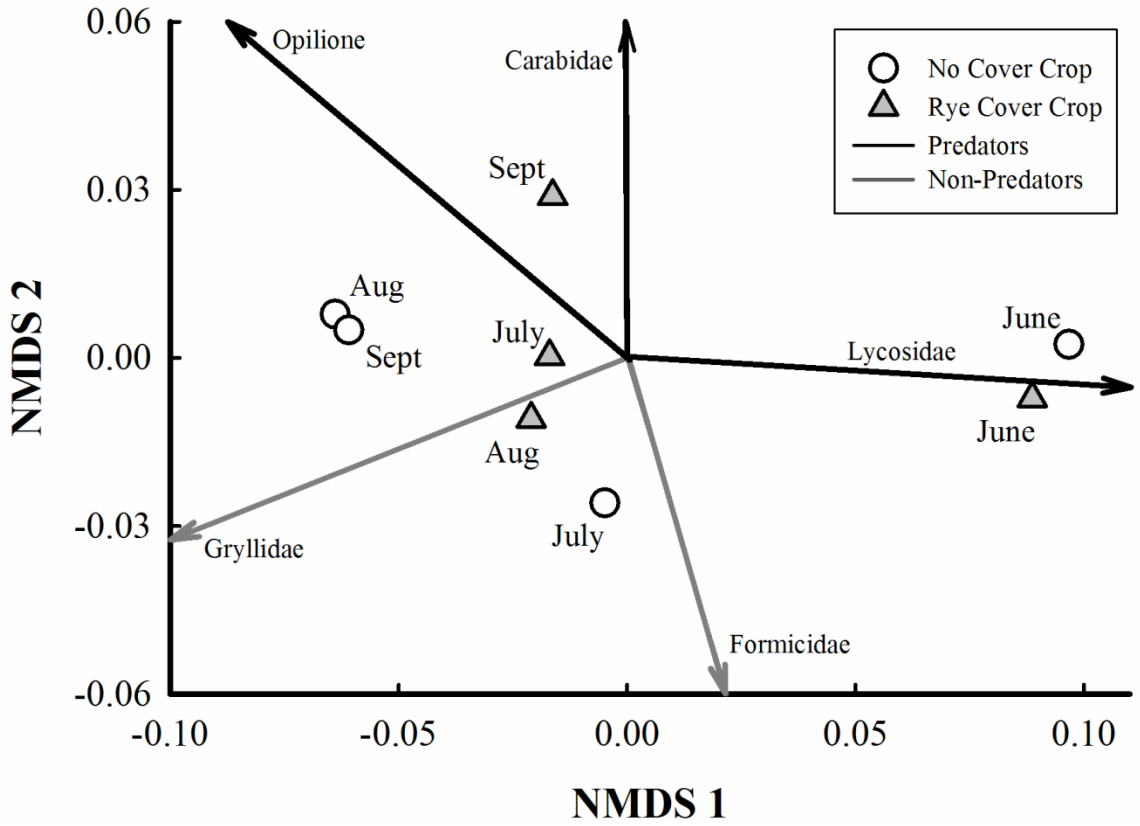

Figure 1A. Nonmetric multidimensional scaling (NMDS) of beneficial arthropod community composition as captured by pitfall traps in corn plots (A). Centroid points represent mean community composition for each cover treatment by sampling date combination. Mean activity-density of all beneficial taxa, predators, and non-predators as captured by pitfall traps from corn plots by sampling date (B). Bar height represent sample means and error bars are the standard error of the mean. Letters denote significant differences in activity-density among sampling dates within groups.

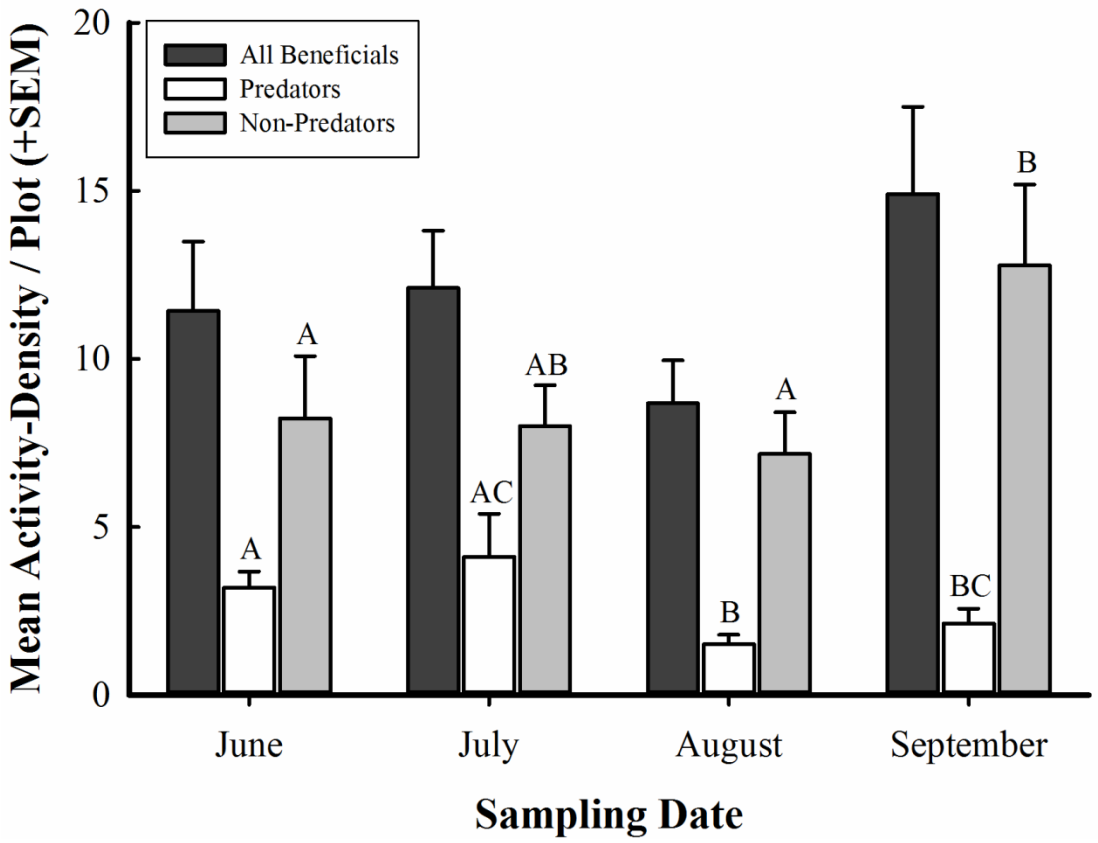

Figure 1B. Nonmetric multidimensional scaling (NMDS) of beneficial arthropod community composition as captured by pitfall traps in corn plots (A). Centroid points represent mean community composition for each cover treatment by sampling date combination. Mean activity-density of all beneficial taxa, predators, and non-predators as captured by pitfall traps from corn plots by sampling date (B). Bar height represent sample means and error bars are the standard error of the mean. Letters denote significant differences in activity-density among sampling dates within groups.

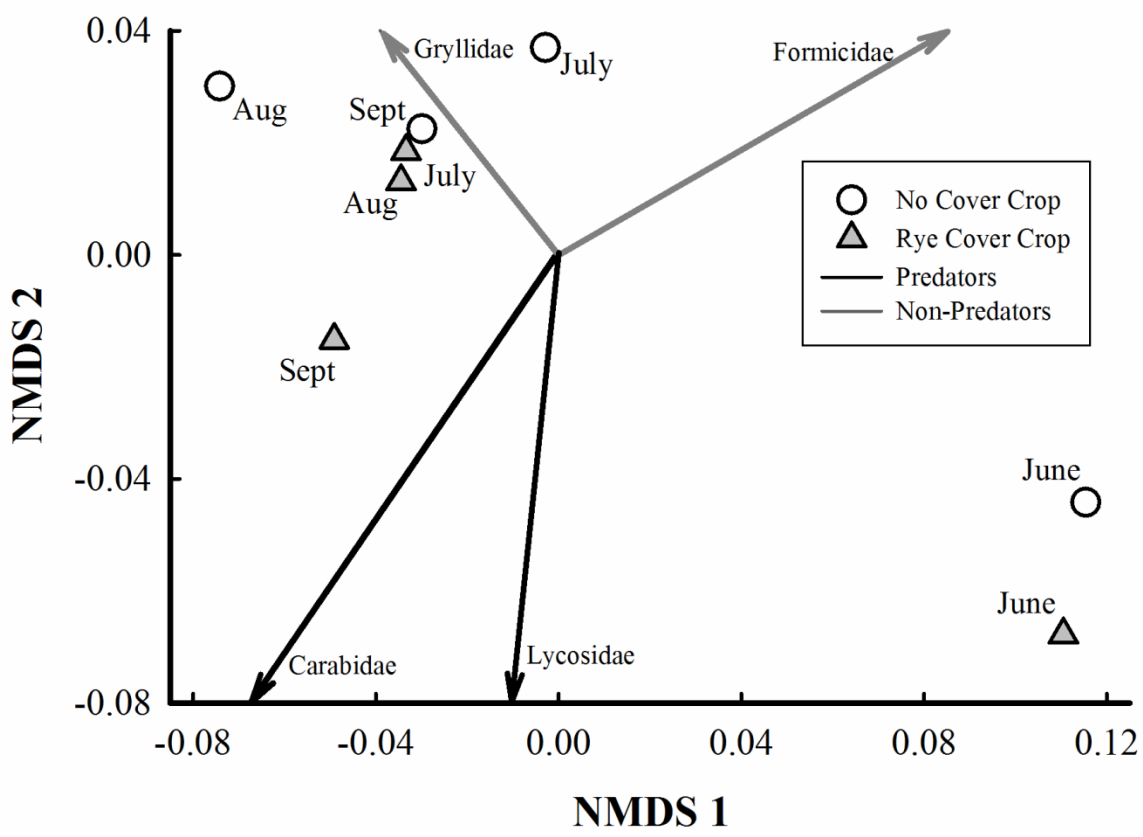

Figure 2A. Nonmetric multidimensional scaling (NMDS) of beneficial arthropod community composition as captured by pitfall traps in soybean plots (A). Centroid points represent mean community composition for each cover treatment by sampling date combination. Mean activity-density of all beneficial taxa, predators, and non-predators as captured by pitfall traps from soybean plots by sampling date (B). Bar height represent sample means and error bars are the standard error of the mean. Letters denote significant differences in activity-density among sampling dates within groups.

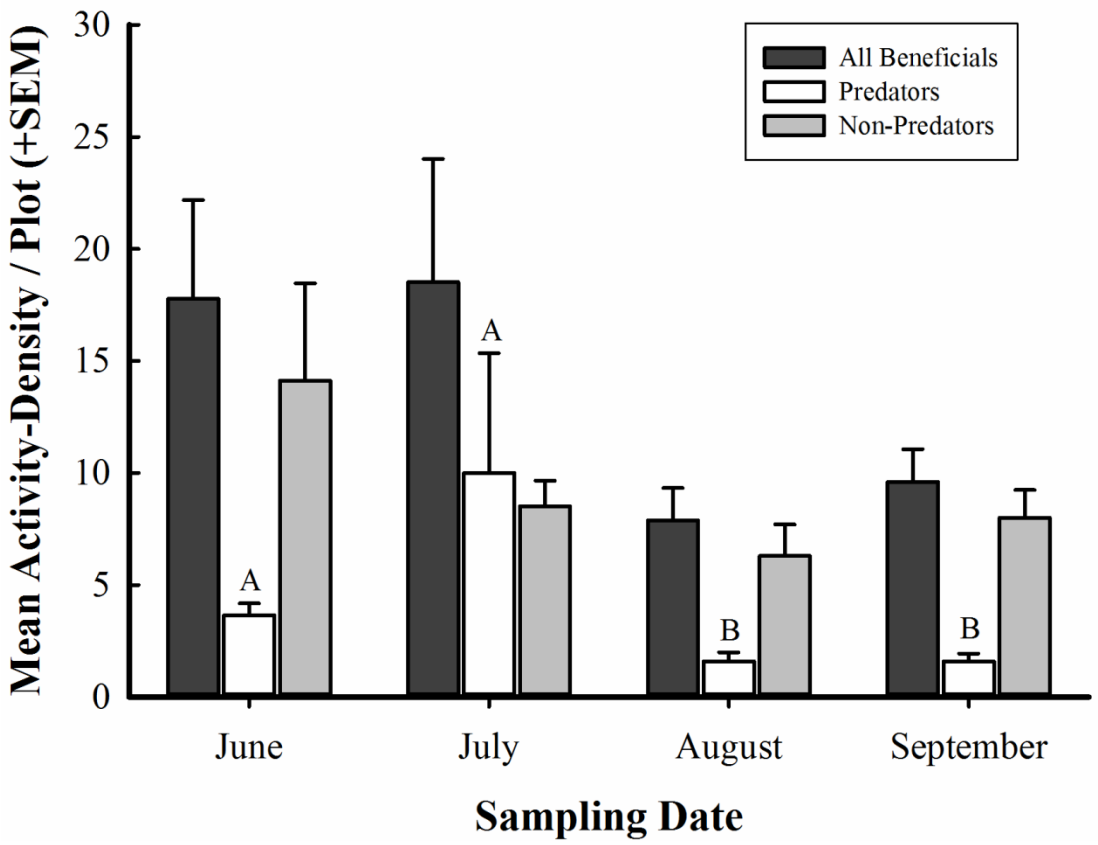

Figure 2B. Nonmetric multidimensional scaling (NMDS) of beneficial arthropod community composition as captured by pitfall traps in soybean plots (A). Centroid points represent mean community composition for each cover treatment by sampling date combination. Mean activity-density of all beneficial taxa, predators, and non-predators as captured by pitfall traps from soybean plots by sampling date (B). Bar height represent sample means and error bars are the standard error of the mean. Letters denote significant differences in activity-density among sampling dates within groups.

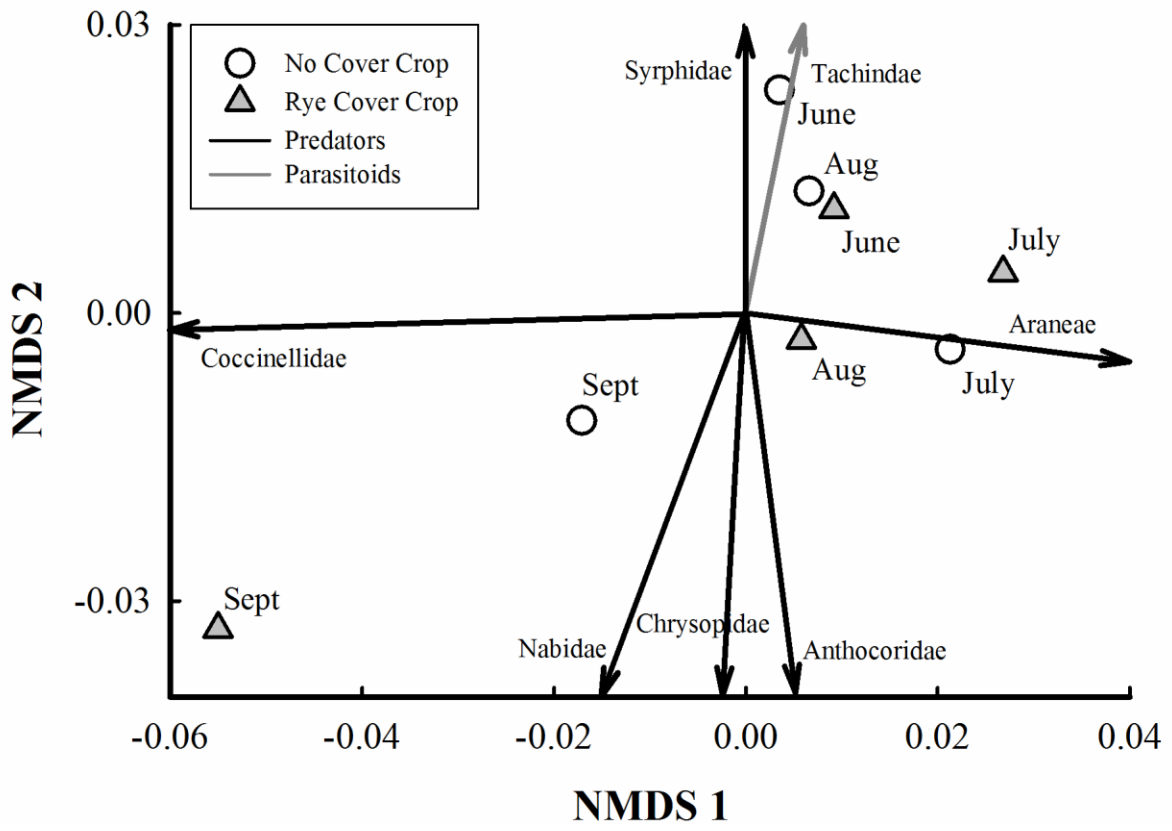

Figure 3A. Nonmetric multidimensional scaling (NMDS) of beneficial arthropod community composition as captured by sweep net sampling in soybean plots (A). Centroid points represent mean community composition for each cover treatment by sampling date combination. Mean abundance of all beneficial taxa, predators, and parasitoids as captured by sweep net sampling from soybean plots by sampling date (B). Bar height represent sample means and error bars are the standard error of the mean. Letters denote significant differences in activity density among sampling dates within groups.

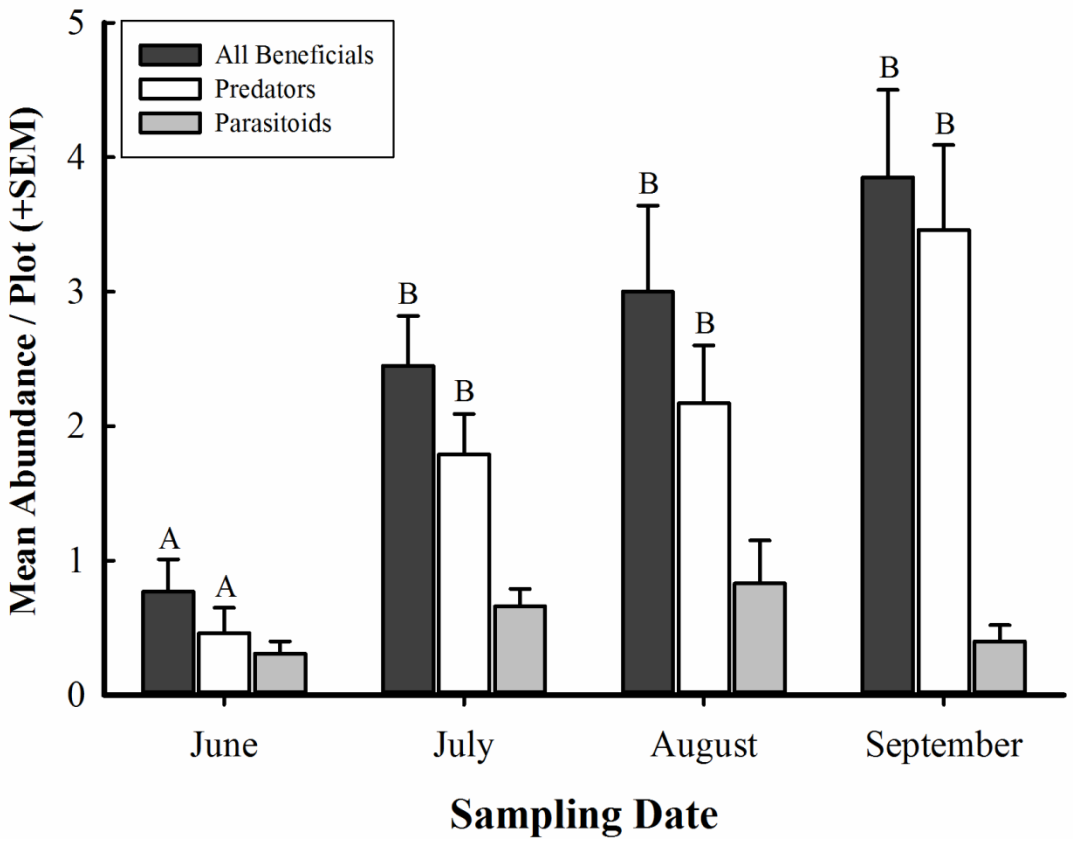

Figure 3B. Nonmetric multidimensional scaling (NMDS) of beneficial arthropod community composition as captured by sweep net sampling in soybean plots (A). Centroid points represent mean community composition for each cover treatment by sampling date combination. Mean abundance of all beneficial taxa, predators, and parasitoids as captured by sweep net sampling from soybean plots by sampling date (B). Bar height represent sample means and error bars are the standard error of the mean. Letters denote significant differences in activity density among sampling dates within groups.

Supplemental Table S1. Analysis of variance of individual taxa captured from corn and soybean plots by sampling method and crop

Sampling Method/ Crop	Group/ Taxa	Cover Treatment			Sampling Date			Trt*Date		
		F	**df**	***P***	***F***	**df**	***P***	***F***	**df**	***P***
Pitfall trap / Corn	Predators									
	Opiliones	0.08	1, 40	0.78	7.38	3, 135	**0.0001**	0.46	3, 135	0.71
	Lycosidae	0.04	1, 40	0.84	8.21	3, 135	**<0.0001**	0.48	3, 135	0.70
	Carabidae	0.94	1, 40	0.34	7.11	3, 135	**0.0002**	0.21	3, 135	0.89
	Non-Predators									
	Gryllidae	0.76	1, 40	0.39	10.06	3, 135	**<0.0001**	1.58	3, 135	0.20
	Formicidae	0.09	1, 40	0.77	9.62	3, 135	**<0.0001**	1.30	3, 135	0.28
	Diplopoda	2.04	1, 40	0.16	34.32	3, 135	**<0.0001**	0.80	3, 135	0.50
Pitfall trap / Soybean	Predators									
	Lycosidae	2.36	1, 41	0.13	6.09	3, 136	**0.0006**	0.52	3, 136	0.67
	Carabidae	6.66	1, 41	**0.013**	7.38	3, 136	**0.0001**	2.27	3, 136	0.08
	Non-Predators									
	Gryllidae	5.58	1, 41	**0.023**	20.67	3, 136	**<0.0001**	0.36	3, 136	0.78
	Formicidae	0.01	1, 41	0.92	15.35	3, 136	**<0.0001**	0.87	3, 136	0.46
	Diplopoda	0.30	1, 41	0.59	18.29	3, 136	**<0.0001**	1.67	3, 136	0.18

Supplemental Table S1 Continued. Analysis of variance of individual taxa captured from corn and soybean plots by sampling method and crop

Sampling Method/ Crop	Group/ Taxa	Cover Treatment			Sampling Date			Trt*Date		
		F	**df**	***P***	***F***	**df**	***P***	***F***	**df**	***P***
Sweep net / Soybean	Predators									
	Araneae	0.94	1, 41	0.34	4.49	3, 137	**0.005**	0.77	3, 137	0.51
	Anthocoridae	0.21	1, 41	0.65	2.93	3, 137	**0.036**	0.33	3, 137	0.80
	Nabidae	1.08	1, 41	0.30	7.12	3, 137	**0.0002**	0.54	3, 137	0.66
	Chrysopidae	0.86	1, 41	0.36	8.72	3, 137	**<0.0001**	2.60	3, 137	0.06
	Coccinellidae	0.07	1, 41	0.79	5.56	3, 137	**0.001**	0.73	3, 137	0.54
	Syrphidae	2.59	1, 41	0.12	2.14	3, 137	0.10	0.07	3, 137	0.98
	Parasitoids									
	Chalcidoidea	0.01	1, 41	0.94	4.56	3, 137	**0.004**	1.31	3, 137	0.27
	Tachinidae	0.39	1, 41	0.54	1.71	3, 137	0.17	0.80	3, 137	0.50

CHAPTER 3

IMPACTS OF ROTATION SCHEMES ON EPIGEAL BENEFICIAL ARTHROPODS

A paper submitted to *Environmental Entomology*

Mike W. Dunbar, Aaron J. Gassmann and Matthew E. O'Neal

Abstract

In agroecosystems, natural enemies that provide biological control of pests respond positively to greater vegetational diversity because it provides alternate food resources, favorable microclimates and refuge from environmental or anthropogenic disturbances. Crop rotation alters agroecosystem diversity both spatially and temporally, and increasing crop diversity within rotation schemes can increase crop yields and reduce reliance on chemical inputs. We hypothesized that increased crop diversity within rotation schemes would positively affect epigeal, beneficial arthropod communities. During 2012 and 2013, pitfall traps were used to measure epigeal communities within three long term crop rotation studies located in Wisconsin and Illinois. Rotation schemes sampled included continuous corn, annually rotated corn and soybean, and an extended rotation of corn, soybean, and wheat. Insects captured were identified to family, and non-insect arthropods were identified to class, order, or family depending upon the taxa. Beneficial arthropods captured included natural enemies, granivores, and detritivores. Epigeal community composition and the activity-density of individual taxa were significantly affected by sampling date, however rotation schemes had no effect on the community composition or individual taxa. Crop species within all three rotations schemes were annual crops, and are associated with agricultural practices

that make infield habitat subject to anthropogenic disturbances and temporally unstable. Habitat instability and disturbance can limit the effectiveness and retention of beneficial arthropods, including natural enemies, granivores and detritivores. Increasing non-crop and perennial species within landscapes in conjunction with more diverse rotation schemes may increase the effect of biological control of pests by natural enemies.

Introduction

Arthropods provide many types of ecosystem services, including biological control of pests (Losey and Vaughan 2006). In agroecosystems, natural enemies are more abundant in diverse agroecosystems compared to monocultures (Landis et al. 2000, Langellotto and Denno 2004, Letourneau et al. 2011). Greater natural enemy abundance has been hypothesized as one of the potential explanations for observed pest abundance reductions in agroecosystems with more vegetational diversity (Root 1973, Andow 1991). Diversity within agroecosystems can be altered by farming practices within crop fields (i.e., intercropping, cover crops, beetle banks) or by changes in landscape heterogeneity (i.e., composition and connectivity among fields). Vegetational diversity also can vary temporally; crops and non-crops may overlap completely in time (i.e., intercropping and living-mulch cover crops) or they may be separated entirely by time (i.e., traditional crop rotation schemes).

Crop rotation alters agroecosystem diversity, both spatially and temporally, and is associated with numerous agronomic benefits. Annual rotation of corn (*Zea mays* L.) and soybean (*Gylcine max* L.) can significantly increase corn yield compared to corn planted continuously, even when continuous corn receives greater rates of fertilizers and pesticides (Bullock 1992). Adding additional crops to rotation schemes can further increase yields and reduce reliance on chemical inputs (Smith et al. 2008). For example, conventionally managed

corn and soybean in a two-year rotation was not as profitable or productive as a extended three-year rotation that added small grains (oat (*Avena sativa* L.) or spring triticale (*Triticosecale* L.)) or a four-year rotation that added small grains and alfalfa (*Medicago sativa* L.) (Davis et al. 2012).

Increasing the diversity of crops within rotation schemes would correspondingly increase agroecosystem diversity, particularly in the U.S. Corn Belt which is dominated by production of corn and soybean (USDA, NASS 2015). Natural enemies that provide biological control of pests are positively affected by greater vegetational diversity because it can offer better alternate food resources, favorable microclimates, and refuge from environmental or anthropogenic disturbances (Marion and Landis 1996, Landis et al. 2000, Sunderland and Samu 2000, Symondson et al. 2002, Gardiner et al. 2009a). Within the Corn Belt, more diverse landscapes provided greater biological control of the soybean pest *Aphis glycines* M. (Hemiptera: Aphididae), soybean aphid, compared to landscapes that were predominately corn and soybean (Gardiner et al. 2009a). Furthermore, landscape vegetational diversity and structure also influenced the composition of *A. glycines* predator communities (Gardiner et al. 2009b).

Low crop diversity and increased farming efficiency together limit the heterogeneity of crop management practices and promote temporal uniformity among fields (Benton et al. 2003). Management practices associated with annual crops (i.e., planting, tillage, harvesting, pesticide applications) regularly disturb habitat and disrupt the effectiveness of natural enemies (Altieri 1999, Landis et al. 2000) and other types of beneficial arthropods, including granivores and detritivores (Robertson et al. 1994, Cromar et al. 1999, Baraibar et al. 2009). The goals of this study were to quantify the effects of rotation schemes that vary in the

diversity of crops planted on the composition of epigeal, beneficial arthropods. We hypothesized that rotation schemes that included greater crop diversity would positively affect beneficial arthropod communities and individual taxa. To test this hypothesis, pitfall traps were used to measure the activity-density of arthropods found in plots of corn without rotation, corn and soybean in annual rotation, and corn and soybean in an extended three-year rotation of corn, soybean, and wheat.

Materials and Methods

Field Sites and Experimental Design. Data were collected during 2012 and 2013 from three locations; the University of Wisconsin Arlington Agricultural Research Station (Arlington, WI; 42º18´ N, 89º20´ W), the University of Wisconsin Lancaster Agricultural Research Station (Lancaster, WI; 42º49´ N, 90º47´ W), and the Northwestern Illinois Agricultural Research and Demonstration Center (Monmouth, IL; 40º55´ N, 90º43´ W). Experimental plots were established to study the long term effects of crop rotation beginning at Arlington in 1986 (Lund et al. 1993, Pedersen and Lauer 2002), at Lancaster in 1966 (Stanger et al. 2008), and at Monmouth in 1996 (Zuber et al. 2015). Plot sizes were 18.2 m × 18.2 m, 6.1 m × 9.1 m, and 22 m × 12 m for Arlington, Lancaster, and Monmouth, respectively. Continuous corn, corn and soybean in an annual rotation, and corn, soybean, and wheat (*Triticum aestivum* L.) in a three-year (extended) rotation were grown at each location and replicated in randomized complete block design. Each crop within the three rotation schemes was present within each block, at all locations every year.

Arthropod Sampling. At each location, six corn and four soybean plots were sampled. Epigeal arthropods were sampled from two plots per crop per rotation scheme; 1) continuously planted corn, 2) annually rotated corn and soybean (both crops sampled) and 3)

an extended, three-year rotation of corn, soybean, and wheat (only corn and soybean were sampled). Plots were sampled four times each year and sampling dates were designated as June (sampled between 23 June and 5 July), July (sampled between 13 and 26 July), August (sampled between 13 and 16 August) and September (sampled between 4 and 13 September).

Three pitfall traps were placed within each plot to estimate the activity-density of epigeal arthropods. Pitfall traps were 1 L cups (Reynolds Food Packaging, Shepherdsville, Kentucky) buried in the ground flush with the soil surface. Traps were filled with ca. 100 mL of non-scented, soapy water solution to prevent arthropods from escaping. To avoid debris entering pitfall traps, a cover raised ca. 5 cm above the soil surface was placed above each trap (Hummel et al. 2012). Pitfall traps remained in plots for 24 h during each sampling period. The recovered contents of pitfall traps were placed separately into sealable plastic bags and stored in freezers until contents were sorted. Taxa classified as beneficial included natural enemies of pests, granivores, and detritivores. Beneficial insects captured in pitfall traps were identified to family, and beneficial non-insect arthropods were identified to class, order, or family depending upon the taxa (Table 1).

Statistical Analysis. In all cases, data were analyzed separately by crop. Taxa were only included in analyses if they composed > 1% of the total number of individuals captured. Data were analyzed with nonmetric multidimensional scaling (NMDS), multivariate analysis of variance (MANOVA) and analysis of variance (ANOVA). Factors tested included rotation scheme, sampling data, and their interaction. For corn, these rotation schemes were continuous corn, corn in annual rotation and corn in extended rotation. For soybean, rotation schemes included soybean in annual rotation and soybean in extended rotation.

Nonmetric multidimensional scaling was conducted using R 3.1 statistical software (Dixon 2003, Oksanen 2013, R Core Team 2014). The NMDS summarizes the relationships among all variables and displays these relationships in ordination space. Each point within the NMDS represents the composition of a community, and composition becomes increasingly similar as distances among points within the NMDS decreases. Function metaMDS was used to create NMDS ordination plots with Sorensen (Bray-Curtis) distances (Krebs 1999). Stress (*S*) and non-metric fit (r^2), statistics measuring goodness of fit of the NMDS ordination distances to the data dissimilarity, were also computed (Oksanen 2013). The envfit function was used to create centroids of mean community composition for each combination of rotation scheme by sampling date as well as create vectors describing changes in activity-density of individual taxa (Oksanen 2013). The vector direction indicates an increase in activity-density for a taxon. The significance of each vector was calculated from 999 random permutations of these data (Oksanen 2013).

Activity-density of taxa was analyzed with a repeated-measures MANOVA that included the factors of rotation scheme, sampling date, and their interaction (PROC GLM, SAS statistical software version 9.3, SAS Institute, Cary, North Carolina). The repeated-measures analysis was based on a split-plot design (Quinn and Keough 2002). Data were transformed with the function log (x + 1) to increase the normality of the residuals. Fixed effects were rotation scheme, sampling date, the interaction of rotation scheme and sampling date. Random effects were year, location, the interaction of year and location, plot nested within the interaction of year × location × rotation scheme and sampling date × plot nested within year × location × rotation scheme. The inclusion of the sampling date × plot nested

within year × location × rotation scheme term in the model makes this a repeated-measures design.

Activity-density of total beneficial arthropods and individual taxa were analyzed using repeated-measures ANOVA (PROC MIXED) in SAS 9.3. To meet the assumptions of the ANOVA, data were transformed by the log (x + 1) function. Rotation scheme, sampling date, and their interactions were classified as fixed effects. Random effects included year, location, the interaction of year and location, plot nested within the interaction of year × location × rotation scheme and sampling date × plot nested within year × location × rotation scheme, and the use of the later most effects in the model makes this a repeated-measures analysis. When significant effects were present, pairwise comparisons were made using the PDIFF option (in PROC MIXED). Alpha levels were adjusted for multiple comparisons using the Bonferroni correction.

Results

During 2012 and 2013, pitfall traps collected over 3,700 and 2,400 individual beneficial arthropods from corn and soybean plots, respectively. For both corn and soybean, the same six taxa each represented > 1% of all individuals captured (Table 1). The vast majority of beneficial individuals collected from both corn and soybean plots were Carabidae and Formicidae.

Low stress solutions were found for NMDS ordinations for corn plots (S = 0.09; Fig. 1A) and soybean plots (S = 0.07; Fig. 2A), and distances within ordinations were highly correlated to pitfall trap data dissimilarity (non-metric fit r^2 = 0.991 and 0.994 for corn and soybean data, respectively). Epigeal community composition in both corn and soybean plots were not significantly affected by rotation scheme when tested by MANOVA, yet the

composition of both communities did change significantly over time (Table 2; Figs. 1B and 2B). Rotation scheme also did not affect total activity-density in epigeal communities captured from corn or soybean plots when test with ANOVA, but sampling date did significantly affect total activity-density in both crops (Tables 3 and 4). Total activity-density in corn and soybean was significantly greater when sampled in June and lowest during August (Figs. 1B and 2B).

Activity density for individual taxa was not significantly affected by rotation scheme, though there was a marginal effect of rotation scheme on the activity-density of Carabidae captured from corn plots (Tables 3 and 4). Activity-density of Carabidae was numerically greatest in annually rotated corn and lowest in corn within extended rotation (Table 4).

Sampling date significantly affected activity-density of nearly all taxa individually (Table 3). Carabidae was the most frequently captured arthropod in pitfall traps (Table 1), and their activity-density was greatest when sampled during June and July. Though the seasonal pattern of Carabidae activity-density was similar in both corn and soybean plots, there were only significant differences among sampling dates when Carabidae was sampled in corn (Table 3; Figs. 1B and 2B). Formicidae also was common in both corn and soybean epigeal communities (Table 1). Activity-density of Formicidae in corn plots peaked during July and waned as the season progressed (Fig. 1B). In soybean plots, activity-density of Formicidae peaked in June, declined through August, and increased during September (Fig. 2B). Analysis of Gryllidae showed that their activity-density changed significantly over time in both corn and soybean plots (Table 3), however only corn plots had significant pairwise comparisons among sampling dates after adjusting alpha levels for multiple comparisons. Activity-density of Gryllidae in corn plots was greatest during September and lowest during

June (Fig. 1B). Activity-density of Opiliones differed by sampling date in soybean plots (Table 3), with capture in pitfall traps the lowest during June and greatest during July sampling (Fig. 2B). In both corn and soybean plots, activity-density of Lycosidae was significantly higher when sampled during June and then declined as sampling continued throughout the year (Table 3; Figs. 1B and 2B). Activity-density of Diplopoda contrasted with that of Lycosidae, as Diplopoda activity-density was significantly greatest when sampled during September (Table 3; Figs. 1B and 2B).

Vectors describing changes in activity-density of individual taxa from both crops were all significantly correlated to the NMDS ordinations (Table 5). In corn and soybean ordinations, changes in activity-density of Carabidae, Formicidae, Gryllidae and Opiliones were better represented by the NMDS ordinations than that of Lycosidae and Diplopoda (Table 5; Figs. 1A and 2A). Gryllidae and Formicidae vectors in both corn and soybean NMDS were consistent with their corresponding activity-density (i.e., activity-density of Formicidae was greatest when sampled earlier in the season and the Formicidae vectors move towards the early season sampling date centroids in both NMDS). However, not all vectors matched the activity-density patterns of their corresponding taxa. For example, Carabidae in corn plots were captured in significantly greater frequency during July compared to September (Fig. 1B), but the vector describing changes in Carabidae activity-density in the NMDS moves directly away from all July and September community centroids (Fig. 1A).

Discussion

The objective of this study was to measure the effect of increased diversity within rotation schemes on epigeal, beneficial arthropods communities. From two years of data, we

observed no significant differences in community composition or total community activity-density among rotation schemes (Tables 2 and 3). Furthermore, activity-density of individual taxa were not affected by rotation scheme (Tables 3 and 4). These data did not support our hypothesis that rotation schemes with greater diversity would positively affect epigeal communities and individual taxa. Instead, sampling date affected community composition and individual taxa in both corn (Fig. 1B) and soybean plots (Fig. 2B).

Increased vegetational diversity has been shown have positive effects on natural enemy abundance (Letourneau et al. 2011). However, no effects of rotation scheme were observed here on any natural enemy taxa (Tables 2 and 3). This lack of response may by partially due to the taxa captured here belonging to multiple functional groups. Opiliones and Lycosidae are both definitively generalist predators and therefore are natural enemies of pest herbivores (Triplehorn and Johnson 2005, Foelix 2011), yet neither taxa responded to increased temporal diversity (Table 3). In a field study in Iowa, Carabidae community activity-density and species richness were both found to increase with increasing diversity within crop rotations and reduced disturbance regimes (O'Rourke et al. 2006), yet Carabidae capture here only responded marginally to increased diversity within crop rotations (Tables 3 and 4). However, Carabidae are a diverse family with species that can be classified as generalist predators, granivores or omnivores (Kromp 1999), and management practices can differentially affect the proportion of Carabidae from each functional group found within fields (Menalled et al. 2006). Like Carabidae, both Formicidae and Gryllidae can fit into multiple functional groups. Formicidae are primarily classified as granivores (Inouye et al. 1980, Baraibar et al. 2009), but have been grouped as predators and detritivores (Dively and Rose 2003, Bhatti et al. 2005). Gryllidae also are primarily granivores (Carmona et al. 1999,

Westerman et al. 2008), but have been observed as predators and as herbivores (Bechinski et al. 1983, Burges and Hinks 1987, Brust and House 1988). Regardless of the functional group diversity of these taxa, none responded to changes in crop rotation diversity.

Increased crop rotation diversity alone may not affect beneficial taxa if disturbance regimes associated with annual crops are not reduced. The expansion of monocultures typically resulted in the loss of spatial diversity and the reduction of natural habitats (Altieri and Letourneau 1982). Increasing the number of crops included within rotation schemes would increase spatial landscape heterogeneity, especially within the Corn Belt. However, if species added to rotation schemes are annual crops then agroecosystems would remain temporally unstable and subject to anthropogenic disturbances. It is thought that the addition of perennial crops or non-crops to rotation schemes and increased connectivity among more stable habitats would support more robust natural-enemy communities (Altieri and Letourneau 1982, Altieri 1999, Landis et al. 2000). For example, natural enemies overwinter more often in field margins because they provide better overwintering shelter than bare crop fields (Thomas et al. 1992a). Strips of perennial grasses planted throughout agricultural fields (beetle banks) have been shown to increase the availability of stable habitats for predators and increase predator movement throughout fields (Thomas et al. 1992b). Granivores are also affected by disturbance regimes, and post dispersal predation of weed seeds by arthropods can be negatively affected by management practices such as tillage (Cromar et al. 1999).

Though more diverse crop rotations on their own may not positively affect natural enemies or other beneficial arthropods, increasing spatial diversity can still provide benefits to farmers by reducing pest abundance. The resource concentration hypothesis predicts insect herbivores to respond negatively to increased diversification due to lower pest recruitment

and retention (Root 1973, Andow 1991). Increased spatial and temporal diversity in agroecosystems is particularly effective against pests with narrow host ranges and pests with low dispersal distances that overwinter in host crop fields (Andow 1991, Zehnder et al. 2007).

There are potential negative effects associated with crop rotation. Primarily, increasing diversity within crop rotations can reduce the area planted to high value crops (Landis et al. 2000). This drawback can be compounded if extended rotations include non-crop species (Altieri 1994). Another potential downside is pest adaption to crop rotation. For example, *Diabrotica virgifera virgifera* LeConte (Coleoptera: Chrysomelidae), western corn rootworm, and *Diabrotica barberi* Smith & Lawrence (Coleoptera: Chrysomelidae), northern corn rootworm, are two functionally monophagous pests with life cycles closely associated to their host plant corn (Chiang 1973). Crop rotation is one option for farmers to manage corn rootworm populations. However, both pest species have evolved resistance to crop rotation; *D. v. virgifera* adapted behaviorally through a loss of host plant ovipositional fidelity (Levine et al. 2002) and *D. barberi* adapted physiologically with variable length, extended diapause (Krysan et al. 1984, Levine et al. 1992). Furthermore, these adaptations allow each species to circumvent both annual and extended rotation schemes.

Increasing diversity in rotation schemes can benefit farmers by increase crop yields and reducing reliance on chemical inputs (Bullock 1992, Smith et al. 2008, Davis et al. 2012). Results presented here indicated that beneficial, epigeal communities in corn and soybean plots were not affected by altering the number of crops within rotation schemes (Tables 2 and 3). Including additional crops in rotation schemes may still lead to a reduction

of pest recruitment and retention within fields, though to what extent the rotation schemes observe here affect pest abundance was not measured.

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Tables

Table 1. Beneficial taxa captured by pitfall traps from corn and soybean plots

			Total Capture (%)	
Class	**Order**	**Family**	**Corn**	**Soybean**
Diplopoda			113 (3%)	73 (3%)
Arachnida	Opiliones		262 (7%)	129 (5%)
	Araneae	Lycosidae	159 (4%)	133 (5%)
Insecta	Coleoptera	Carabidae	1,746 (45%)	843 (35%)
	Hymenoptera	Formicidae	1,056 (27%)	941 (39%)
	Orthoptera	Gryllidae	377 (10%)	288 (12%)

Table 2. Multivariate analysis of variance of total beneficial arthropods captured from corn and soybean plots

	Corn			**Soybean**		
	F	**df**	***P***	***F***	**df**	***P***
Rotation Scheme	0.54	2, 28	0.59	0.10	1, 17	0.75
Sampling Date	6.19	3, 93	**0.0007**	4.45	3, 58	**0.0070**
Rotation*Date	0.32	6, 93	0.92	0.58	3, 58	0.63

Table 3. Analysis of variance of total beneficial arthropods and individual taxa captured from corn and soybean plots

Crop	Rotation Scheme			Sampling Date			Rotation * Sampling Date		
Taxa	***F***	**df**	***P***	***F***	**df**	***P***	***F***	**df**	***P***
Corn									
Total	0.83	2, 28	0.44	6.64	3, 93	**0.0004**	0.35	6, 93	0.91
Carabidae	2.96	2, 28	0.07	3.11	3, 93	**0.030**	0.77	6, 93	0.60
Formicidae	2.10	2, 28	0.32	11.83	3, 93	**<0.0001**	0.34	6, 93	0.91
Gryllidae	0.73	2, 28	0.49	3.59	3, 93	**0.017**	0.57	6, 93	0.75
Opiliones	0.13	2, 28	0.87	0.31	3, 93	0.82	0.24	6, 93	0.96
Lycosidae	0.78	2, 28	0.47	10.74	3, 93	**<0.0001**	0.55	6, 93	0.77
Diplopoda	0.60	2, 28	0.56	6.80	3, 93	**0.0003**	0.67	6, 93	0.67
Soybean									
Total	0.04	1, 17	0.85	6.08	3, 58	**0.001**	0.12	3, 58	0.95
Carabidae	0.01	1, 17	0.94	2.15	3, 58	0.10	0.13	3, 58	0.94
Formicidae	0.02	1, 17	0.90	8.04	3, 58	**0.0001**	0.57	3, 58	0.64
Gryllidae	0.01	1, 17	0.98	3.23	3, 58	**0.029**	1.07	3, 58	0.37
Opiliones	0.11	1, 17	0.74	4.30	3, 58	**0.008**	0.09	3, 58	0.96
Lycosidae	0.26	1, 17	0.62	4.57	3, 58	**0.006**	0.65	3, 58	0.58
Diplopoda	0.27	1, 17	0.61	5.86	3, 58	**0.001**	0.37	3, 58	0.78

Table 4. Mean activity-density of the total beneficial arthropod community and individual taxa per plot by rotation scheme from corn and soybean plots

Crop	Rotation Scheme (Mean ± SEM)		
Taxa	**Continuous**	**Annual**	**Extended**
Corn			
Total	25.4 ± 3.5	30.2 ± 4.6	25.0 ± 5.0
Carabidae	13.0 ± 2.5	14.0 ± 3.8	11.0 ± 3.9
Formicidae	5.6 ± 1.7	9.2 ± 2.2	8.1 ± 1.8
Gryllidae	3.2 ± 0.8	3.0 ± 0.7	2.0 ± 0.4
Opiliones	1.8 ± 0.3	2.3 ± 0.5	1.6 ± 0.3
Lycosidae	1.0 ± 0.2	1.2 ± 0.2	1.2 ± 0.3
Diplopoda	0.6 ± 0.1	0.8 ± 0.2	1.1 ± 0.3
Soybean			
Total	.	26.2 ± 4.9	28.5 ± 5.5
Carabidae	.	9.2 ± 2.5	10.0 ± 3.1
Formicidae	.	10.3 ± 3.8	11.1 ± 4.1
Gryllidae	.	3.1 ± 0.6	3.5 ± 0.7
Opiliones	.	1.5 ± 0.4	1.5 ± 0.4
Lycosidae	.	1.4 ± 0.3	1.6 ± 0.5
Diplopoda	.	0.7 ± 0.2	1.0 ± 0.3

Table 5. Vector coefficient of determinations for individual taxa within NMDS ordinations by crop

Crop	**Vectors**[a]	
Taxa	**r^2**	***P***
Corn		
Carabidae	0.30	0.001
Formicidae	0.30	0.001
Gryllidae	0.41	0.001
Opiliones	0.23	0.001
Lycosidae	0.06	0.014
Diplopoda	0.13	0.001
Soybean		
Carabidae	0.50	0.001
Formicidae	0.45	0.001
Gryllidae	0.54	0.001
Opiliones	0.30	0.001
Lycosidae	0.07	0.036
Diplopoda	0.07	0.031

[a] Vector statistical significance based on 999 random permutations of the data

Figures

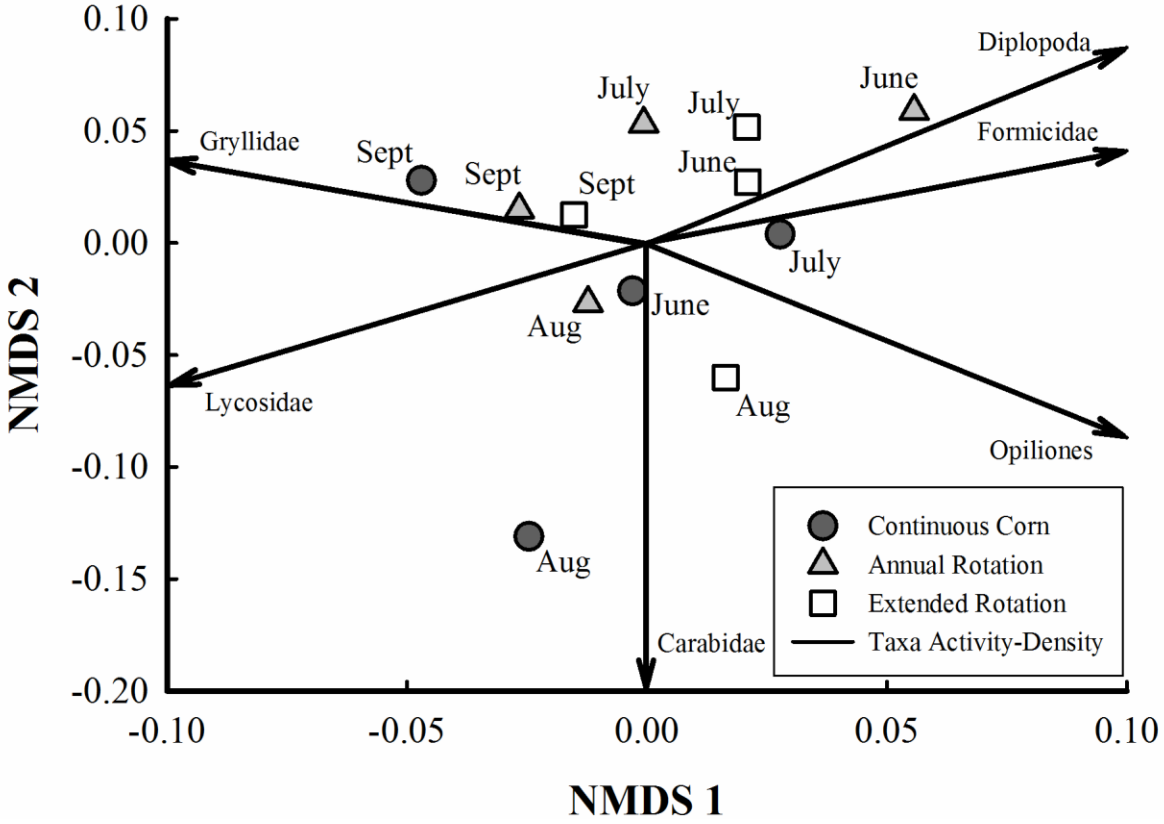

Figure 1A. Nonmetric multidimensional scaling (NMDS) ordination of beneficial arthropod community composition as captured by pitfall traps in corn plots (A). Centroid points represent mean community composition for each rotation scheme by sampling date combination. Mean activity-density of total beneficial arthropods and individual taxa as captured by pitfall traps from corn plots by sampling date (B). Bar height represent sample means and error bars are the standard error of the mean. Letters denote significant differences in activity-density among sampling dates within total beneficial arthropods and each individual taxon.

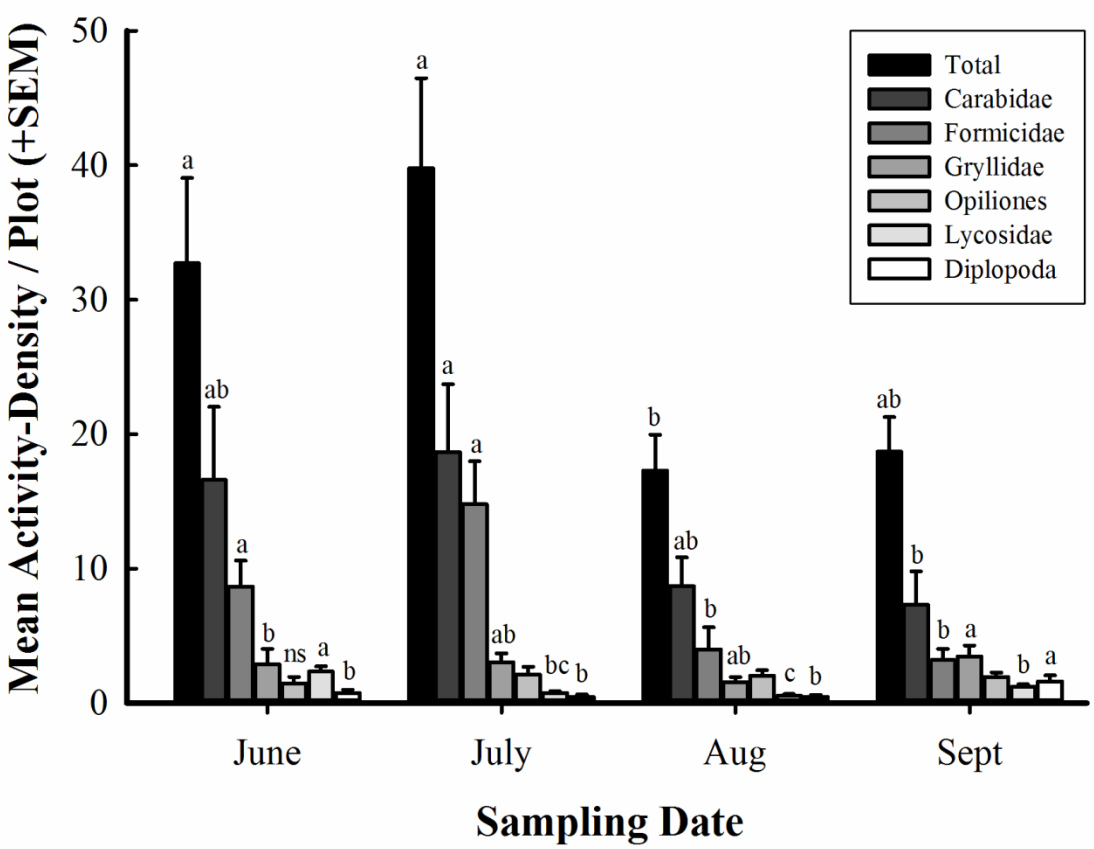

Figure 1B. Nonmetric multidimensional scaling (NMDS) ordination of beneficial arthropod community composition as captured by pitfall traps in corn plots (A). Centroid points represent mean community composition for each rotation scheme by sampling date combination. Mean activity-density of total beneficial arthropods and individual taxa as captured by pitfall traps from corn plots by sampling date (B). Bar height represent sample means and error bars are the standard error of the mean. Letters denote significant differences in activity-density among sampling dates within total beneficial arthropods and each individual taxon.

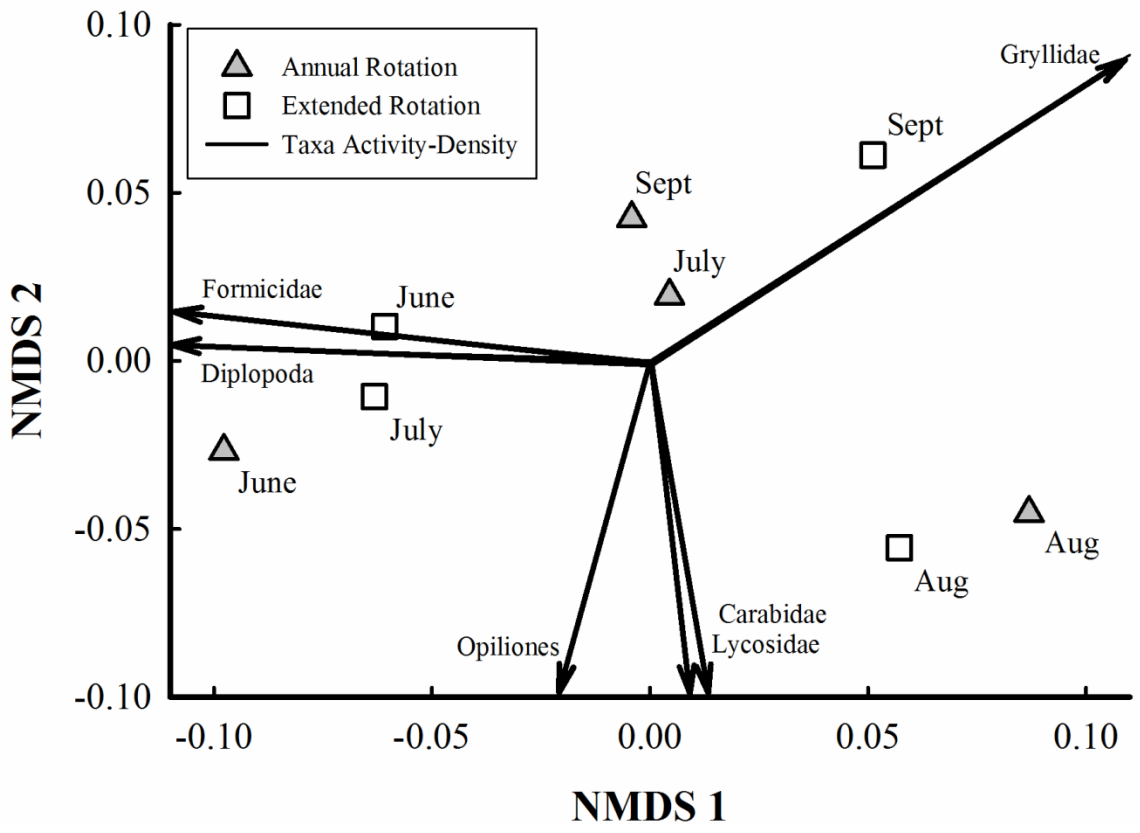

Figure 2A. Nonmetric multidimensional scaling (NMDS) ordination of beneficial arthropod community composition as captured by pitfall traps in soybean plots (A). Centroid points represent mean community composition for each rotation scheme by sampling date combination. Mean activity-density of total beneficial arthropods and individual taxa as captured by pitfall traps from soybean plots by sampling date (B). Bar height represent sample means and error bars are the standard error of the mean. Letters denote significant differences in activity-density among sampling dates within total beneficial arthropods and each individual taxon.

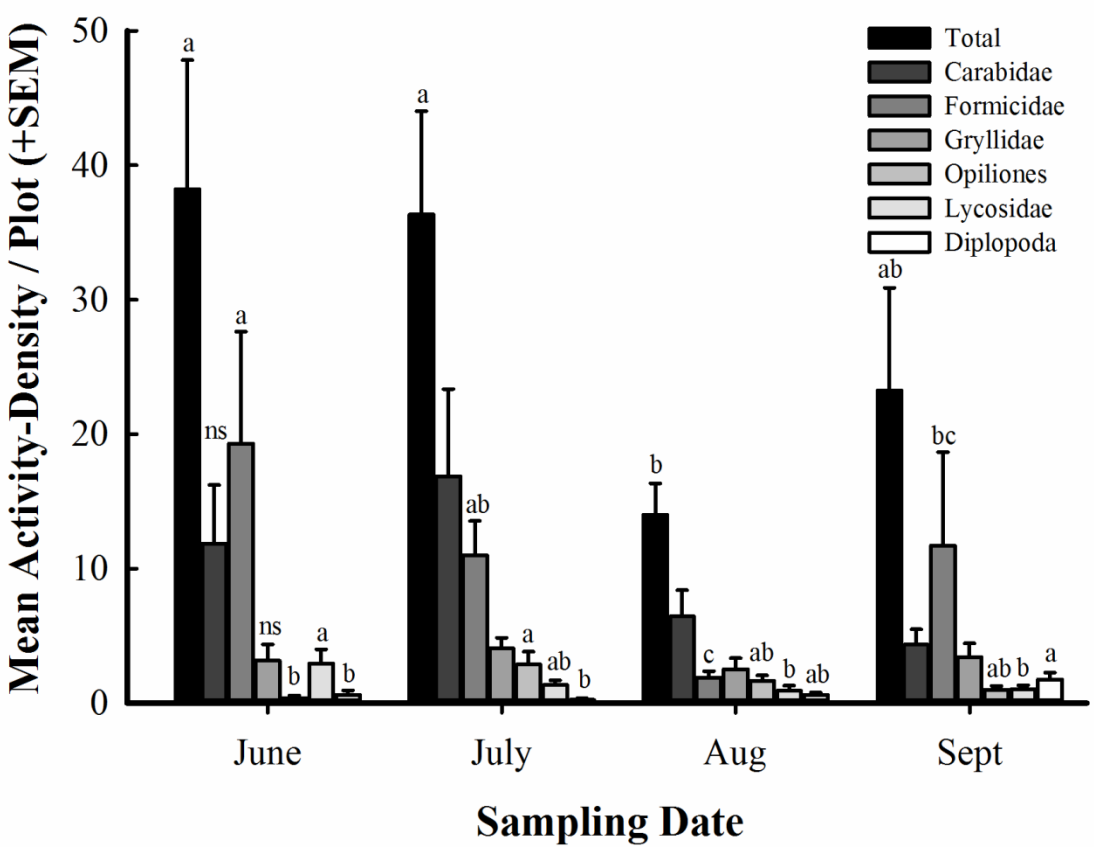

Figure 2B. Nonmetric multidimensional scaling (NMDS) ordination of beneficial arthropod community composition as captured by pitfall traps in soybean plots (A). Centroid points represent mean community composition for each rotation scheme by sampling date combination. Mean activity-density of total beneficial arthropods and individual taxa as captured by pitfall traps from soybean plots by sampling date (B). Bar height represent sample means and error bars are the standard error of the mean. Letters denote significant differences in activity-density among sampling dates within total beneficial arthropods and each individual taxon.

CHAPTER 4.

EFFECTS OF FIELD HISTORY ON ADULT ABUNDANCE OF NORTHERN AND WESTERN CORN ROOTWORM (COLEOPTERA: CHRYSOMELIDAE) AND ROOT INJURY

A paper submitted to *The Journal of Economic Entomology*

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Abstract

Western corn rootworm, *Diabrotica virgifera virgifera* LeConte (Coleoptera: Chrysomelidae), and northern corn rootworm, *Diabrotica barberi* Smith & Lawrence, are major pests of corn (*Zea mays* L.). Corn producing *Bacillus thuringiensis* (Bt) toxins is widely used to manage *Diabrotica* spp., however Bt resistance by *D. v. virgifera* has led to high levels of feeding injury in the field. We tested whether field history affected root injury and abundance of adult *Diabrotica* spp. In 2013 and 2014, four types of cornfields (total n = 47) were sampled: 1) recently rotated fields, 2) continuous cornfields, 3) fields with a history of injury to Bt corn (past problem fields) and 4) fields with greater than one node of injury to Bt corn at the time of sampling (current problem fields). For each field, data were collected on field history, root injury and the abundance of adult *Diabrotica* spp. Root injury and the abundance of *D. v. virgifera* were significantly greater in current problem fields compared to the other field types, and *D. barberi* were significantly more abundant in recently rotated fields. Root injury and the abundance of *D. v. virgifera* did not differ among recently rotated fields, continuous cornfields and past problem fields. Analysis of field history showed that

recently rotated fields were characterized by significantly less Bt corn, soil-applied insecticides and years planted to corn continuously. These results suggest that greater cropping practice diversity can reduce management inputs for *Diabrotica* spp., however, its effects on resistance evolution remain undetermined.

Introduction

Diabrotica virgifera virgifera LeConte (Coleoptera: Chrysomelidae), western corn rootworm, and *Diabrotica barberi* Smith & Lawrence (Coleoptera: Chrysomelidae), northern corn rootworm, are important pests of corn (*Zea mays* L.) in North America. Both species are univoltine with life cycles tightly linked to corn (Chiang 1973, Meinke et al. 2009, Spencer et al. 2009). Adult *D. barberi* and *D. v. virgifera* feed on corn silks, pollen and kernels, although *D. barberi* will readily consume plant material from other species (Lance and Fisher 1987). Eggs are oviposited in the soil of cornfields, diapause through the winter and larvae hatch during the spring. Larvae of both species feed on corn roots and the resulting injury reduces the ability of plants to take up water and nutrients (Levine and Oloumi-Sadeghi 1991). Larval feeding on corn roots is the primary cause of yield loss from *Diabrotica* spp. (Gray et al. 2009), and corn yield is reduced by 15 to 17% for each node of root injury (Dun et al. 2010, Tinsley et al. 2013).

Farmers have several management options to mitigate injury from *Diabrotica* spp. Crop rotation has been used to manage *Diabrotica* spp. for over a century (Spencer et al. 2014), and is effective because larvae that hatch in fields rotated to a non-corn crop starve (Branson and Ortman 1970, 1971). Conventional insecticides have been used for management of *Diabrotica* spp. since the 1940's, and can either be applied to the soil at planting to reduce larval feeding on roots or aerially to both decrease silk feeding and

suppress adult populations and oviposition (Levine and Oloumi-Sadeghi 1991). Since in 2003, genetically modified corn producing insecticidal toxins derived from *Bacillus thuringiensis* (Bt) has been commercially available to manage larval *Diabrotica* spp. (EPA 2003). There are currently four *Diabrotica*-active Bt toxins available, produced in corn either singly or as a pyramid; Cry3Bb1, Cry34/35Ab1, mCry3A and eCry3.1Ab (Cullen et al. 2013).

Integrated Pest Management (IPM) combines multiple management strategies with knowledge of pest ecology to sustainably manage pest populations (Stern et al. 1959). Compared to monocultures, agroecosystems with greater vegetational diversity have been associated with decreased pest recruitment and retention (Andow 1991, Landis et al. 2000), particularly for pests with narrow host ranges (Root 1973). Correspondingly, studies have shown that increasing the diversity or length of crop rotations can reduce reliance on chemical inputs such as pesticides while protecting crop yields (Bullock 1992, Smith et al. 2008, Davis et al. 2012). Additionally, IPM can decrease the intensity of selection pressure on pest populations to evolve resistance to any single strategy by diversifying the causes of pest morality (McGaughey and Whalon 1992).

Bt corn has been widely used by farmers for insect pest management and the rapid adoption of Bt crops has led to concerns over the development of resistant populations (Gould 1998, Onstad et al. 2001, Carriere et al. 2010). Seventy-two percent of corn planted in the U.S. during 2015 produced Bt toxins that targeted pest insects (USDA, NASS 2015), including *D. v. virgifera* and *D. barberi*. Within seven years of commercialization of Bt corn targeting *Diabrotica* spp., cornfields in Iowa were observed with severe root injury associated with field-evolved resistance to Cry3Bb1 by *D. v. virgifera* (Gassmann et al.

2011). More reports of Cry3Bb1 resistance in Iowa, Illinois and Nebraska were soon published (Gassmann et al. 2012, 2014; Gray 2014, Wangila et al. 2015) as well as cross-resistance between Cry3Bb1 and mCry3A toxins (Gassmann et al. 2014, Wangila et al. 2015). At present, there are no reports of field-evolved resistance by *D. v. virgifera* to either Cry34/35Ab1 (Gassmann et al. 2014) or eCry3.1Ab.

As populations of Bt-resistant *D. v. virgifera* continue to develop, management may require more than one tactic to meet this new challenge. Fields with Bt-resistant *D. v. virgifera* were typically characterized by continuous planting of corn and continuous planting of Cry3Bb1 corn (Gassmann et al. 2011, 2012; Wangila et al. 2015). Integrating alternate management tactics for *D. v. virgifera*, such as crop rotation or conventional insecticides, in coordination with Bt crops may mitigate the risk of injury from Cry3Bb1 and mCry3A-resistant *D. v. virgifera* and sustain the efficacy of the remaining Bt toxins (Gassmann 2012, Tabashnik and Gould 2012). Our objectives were to test the effects of field history, including crop rotation and management of *Diabrotica* spp., on root injury and abundance of adult *D. v. virgifera* and *D. barberi*. During 2013 and 2014, we sampled 47 cornfields in Iowa that were either recently rotated (second-year cornfields), planted to long-term continuous corn (> seven years of continuous corn), had previously experienced greater than one node of injury to Bt corn from *D. v. virgifera* or were currently experiencing severe *Diabrotica* spp. injury to Bt corn. We hypothesized that root injury and abundance of adult *Diabrotica* spp. would be reduced in fields with more frequent crop rotation and additional pest management practices compared to fields that lack diverse cropping history. Additionally, we compared how farmers mitigated Bt resistance in cornfields that had previously experienced severe injury to either Cry3Bb1 or mCry3A corn. We hypothesized that farmers would mitigate

management challenges from *D. v. virgifera* by either rotating fields away from corn, changing the variety of Bt corn planted, applying more conventional insecticides or some combination of these factors.

Materials and Methods

Field Selection. In 2013 and 2014, cornfields in Iowa were sampled to measure root injury from larval *Diabrotica* spp. and the abundance of adult *D. barberi* and *D. v. virgifera* (Fig. 1). Fields were identified by Iowa State University regional agronomists and local cooperators. The fields sampled fit into one of four types; 1) recently rotated fields that were planted to corn for the second consecutive year at the time of a sampling, 2) continuous cornfields were fields planted to corn for a minimum of seven consecutive years, 3) past problem cornfields were fields that had been previously sampled for root injury and had greater than expected injury (> 1 node of root injury (EPA 2011)) to either Cry3Bb1 corn (n = 11) or mCry3A corn (n = 2), as measured by the 0 to 3 root-node injury scale (Oleson et al. 2005), and had been planted to corn for at least two years at the time of sampling, and 4) current problem fields that were fields with greater than expected injury to Bt corn (> 1 node of root injury) during the year the field was sampled, which was either 2013 or 2014. Cooperating farmers identified recently rotated fields and continuous cornfields based solely on cropping history (i.e., 2nd-year or > 7 year cornfields), independent of previous *Diabrotica* spp. injury or pest management practice. Past problem fields were initially sampled between 2009 and 2013, and roots sampled from these fields (10.8 ± 1.2 roots per field, mean ± SEM) scored on average 2.1 ± 1.2 nodes of root injured (mean injury score per field ranged from 1.56 to 2.91).

Data Collection. Farmers were asked to provide a history of the crops planted and management practices used for *Diabrotica* spp. in each field. When possible, these field histories were collected starting from the year sampled through 2003 (the commercial introduction of Bt corn targeting *Diabrotica* spp.). Data collected included the crop planted each year, and in years when corn was planted, whether a Bt trait was planted (if yes, which trait) and if a soil or foliar applied insecticide was used to manage *Diabrotica* spp.

Adult *Diabrotica* spp. were sampled from cornfields with unbaited Pherocon AM yellow sticky traps (referred to as sticky traps; Trece Inc., Adair, OK) using methods similar to Dunbar and Gassmann (2013). Twelve sticky traps were placed within each cornfield and arranged in two transects. Transects were separated by a minimum of 100 m and kept 50 m from any field edge. Sticky traps were stationed at 20 m intervals along each transect and were attached to corn plants at ear height. Traps were placed in cornfields throughout the first three weeks of August, and were changed weekly throughout this period.

Twelve roots were sampled from the interior of each cornfield during August. Roots were sampled along the same transects that were used for sticky traps. Corn roots were sampled from plants 1.5 m distant from the corn plant holding a sticky trap. Mean root injury was quantified based on the 0 to 3 node-injury scale (Oleson et al. 2005) from all 12 roots sampled. Some fields visited as current problem fields had mean node-injury scores of less than 1 node, and these fields were therefore excluded from further analyses (4 of 9 fields in 2013 and 1 of 5 sampled fields in 2014). Corn roots were tested for the presence of *Diabrotica* spp. active Bt toxin with an ELISA kit (Envirologix, Portland, Maine). In 2013, all 12 roots from each field were tested for Cry3Bb1, Cry34/35Ab1 and mCry3A toxins. In

2014, the presence of each Bt toxin (Cry3Bb1, Cry34/35Ab1, mCry3A and eCry3.1Ab) was tested from a random subset of corn roots (mean subset = 6.7 per Bt toxin, SEM = 0.16).

Data Analysis. For each field and each week sampled, the total number of *D. barberi* and *D. v. virgifera* captured by each sticky trap was counted. The total number of each species was then averaged among the 12 sticky traps placed within each field for a sampling week. The average *D. barberi* and *D. v. virgifera* captured per sticky trap per sampling week was divided by the number of days sticky traps were in the field to calculate the average *D. barberi* and *D. v. virgifera* captured per sticky trap per day for each week sampled. Data from the week with the highest capture of *D. barberi* and *D. v. virgifera* captured per sticky trap per day, which we defined as peak abundance, was use for all analyses.

Root injury, peak abundance of *D. v. virgifera* and peak abundance of *D. barberi* were analyzed separately per year with mixed-model analysis of variance (ANOVA) using PROC MIXED in SAS 9.3 (SAS Institute, Cary, North Carolina). To ensure normality of the residuals, peak abundance of *D. barberi* and peak abundance of *D. v. virgifera* were transformed by the function square root (x) and root injury data by the function log (x). In the analysis, field type was a fixed effect and random effects included 1) location nested within field type and 2) sticky trap or root nested within location × field type. Additionally for each field, the ratio of *D. v. virgifera* to *D. barberi* was calculated by dividing the total number of *D. v. virgifera* by the total number of *D. barberi* captured from all sticky traps from all weeks sampled. Ratios were compared among field types, separately by year, using mixed-model ANOVA (PROC MIXED). Data were transformed by the function log (x) to ensure normality of the residuals.

Field type was a fixed effect in the analysis and location nested within field type was the random effect. When significant effects were present in a model, pairwise comparisons were made using the PDIFF option in PROC MIXED and alpha levels were adjusted for multiple comparisons using the Bonferroni correction.

To compare the field history data among field types, we used the proportion of years a field was planted to corn, planted to corn continuously (i.e., the number of years in which corn was grown for two or more years consecutively) and received other management practices for *Diabrotica* spp. (i.e., Cry3Bb1 corn or soil-applied insecticide). Fields where less than 75% of the field history was known were excluded from further analyses (n = 10 fields excluded) (Supp. Tables S1, S2, S3 and S4). The percentage of field history known for each field was calculated as the # of complete years of field history / the total # years (i.e., 11 years for fields sampled in 2013 and 12 years for fields sampled during 2014). When field histories were not complete, crops planted within fields for all unknown years were identified using CropScape- cropland data layer (USDA, NASS 2016). A year where a field was planted to corn was complete if the type of Bt corn planted and the use of soil and foliar applied insecticide were known. Years could also be scored as partially complete (e.g., unknown Bt corn, known use of soil insecticide, known use of foliar insecticide = a 0.66 complete year), and this was counted in the calculation of whether or not field history was 75% complete. A year where a field was planted to a known non-corn crop was viewed as complete. For fields included in the analysis that were missing data on management tactics for some years, management tactics were assumed to occur with the same frequency in years with missing data as they did for years which a field history was known.

Multiple regressing analysis (PROC REG) was used to test the effect of field history on root injury, peak abundance of *D. v. virgifera,* peak abundance of *D. barberi* and the ratio of *D. v. virgifera* to *D. barberi*. Root injury and adult *Diabrotica* spp. data from 2013 and 2014 were combined and transformed by the function log (x). Forward and backward stepwise section (SELECTION = STEPWISE) was used for excluding ($P > 0.15$) and including ($P < 0.15$) variables in the model (Littell et al. 1996). Factors used in regression analyses included each field type, the management practices used for *Diabrotica* spp. during the year a field was sampled (i.e., non-Bt, Cry3Bb1, Cry34/35Ab1, mCry3A or Cry3Bb1 + Cry34/35Ab1 corn; application of soil or foliar insecticide), and the proportions of years each field was: 1) planted to corn, 2) planted corn continuously, 3) planted to a specific Bt corn (Cry3Bb1, Cry34/35Ab1, mCry3A or Cry3Bb1 + Cry34/35Ab1), 4) planted to non-Bt corn, 5) treated with soil-applied insecticide and 6) treated with foliar-applied insecticide.

Field histories were compared among field types with mixed-model ANOVA (PROC MIXED). Factors tested were the proportions of years a field was: 1) planted to corn, 2) planted to corn continuously, 3) planted to non-Bt corn, 4) planted to a specific type of Bt corn (Cry3Bb1, Cry34/35Ab1, mCry3A or Cry3Bb1 + Cry34/35Ab1), 5) treated with soil-applied insecticide and 6) treated with foliar-applied insecticide. For the analysis of field histories among field types, field type was a fixed effect and the random effect was location nested within field type. When significant effects were present, pairwise comparisons were made using the PDIFF option in PROC MIXED and alpha levels were adjusted for multiple comparisons using the Bonferroni correction. Additional analyses were separately conducted to compare field histories of past problem fields between the time before and after greater than expected injury to Bt corn was observed. Factors tested were the same as the analysis of

field histories compared among field types. Frequency of use for each management tactic was compared before and after greater than expected injury with a paired two-tailed *t*-test (PROC TTEST).

Results

Field Sites. Of the 47 cornfields sampled in 2013 and 2014, 89% were planted to Bt corn (Table 1). Most cornfields were planted to pyramided Bt corn producing Cry3Bb1 and Cry34/35Ab1 toxins (47%), followed by Cry3Bb1 corn (21%), Cry34/35Ab1 corn (15%), non-Bt corn (11%) and mCry3A corn (6%). Soil insecticide was applied to 25% of all cornfields, of which 83% of those fields with soil insecticide were also planted to Bt corn. Eleven of the 13 past problem fields were planted to pyramided corn, and soil insecticide was applied to 45% those fields with pyramided Bt corn. Current problem cornfields were all planted to single trait Bt corn, expressing either Cry3Bb1 (78%) or mCry3A (22%), without soil insecticide.

Root Injury. Root injury differed significantly among field types in both 2013 and 2014 (Fig. 2). In 2013, current problem fields had significantly greater feeding injury to roots compared to all other field types ($F = 12.4$; df = 3, 16; $P = 0.0002$); root injury in current problem fields averaged over two nodes destroyed by larval feeding. The pattern of root injury among field types was similar in 2014. Current problem fields had significantly more root injury compared to the other field types ($F = 26.2$; df = 3, 23; $P < 0.0001$). Roots from recently rotated fields, continuous cornfields and past problem fields had very little injury and did not differ significantly from each other in either year.

Adult Abundance. Peak abundance of *D. v. virgifera* in 2013 was significantly greater in current problem fields compared all other field types ($F = 18.8$; df = 3, 16; $P <$

0.0001) (Fig. 3). Peak abundance of *D. v. virgifera* in recently rotated fields, continuous cornfields and past problem fields did not differ from one another. In 2014, peak abundance of *D. v. virgifera* was significantly greater in current problem fields compared to the other field types (F = 9.0; df = 3, 23; P = 0.0004) (Fig. 3), with no significant differences among recently rotated fields, continuous cornfields and past problem fields.

Peak abundance of *D. barberi* differed significantly among field types in 2013 (F = 6.1; df = 3, 16; P = 0.006) (Fig. 4). Recently rotated fields and continuous cornfields had significantly greater peak abundance of *D. barberi* compared to current problem fields, and peak abundance in past problem fields did not differ from any other field type. Peak abundance of *D. barberi* did not differ among field types in 2014 (F = 0.6; df = 3, 23; P = 0.62) (Fig. 4).

The ratio of *D. v. virgifera* to *D. barberi* within cornfields differed significantly among field types in 2013 (F = 9.5; df = 3, 16; P = 0.0008) and in 2014 (F = 5.1 df = 3, 23; P = 0.007). In 2013, current problem fields had a significantly greater ratio of *D. v. virgifera* to *D. barberi* than the other field types, but no differences were detected among recently rotated fields, continuous cornfields and past problem fields (Table 2). In 2014, current problem fields had a significantly greater ratio of *D. v. virgifera* to *D. barberi* than recently rotated fields, while continuous cornfields and past problem fields were intermediate and did not differ statistically (Table 2).

Field History. Multiple regression analysis of field history explained 59% of the observed variation in root injury (Table 3). The only parameter retained in the model was current problem fields, which was positively correlated with root injury. Multiple regression analysis explained 51% of the variation in the abundance of *D. v. virgifera*, and the model

retained the parameters of current problem fields and fields planted to Cry34/35Ab1 corn during the year the field was sampled (Table 3). Both parameters were positively correlated with abundance of *D. v. virgifera*. Forty-four percent of the abundance of *D. barberi* was explained in multiple regression analysis (Table 3), and parameters retained in the model were continuous cornfields and years planted to corn continuously. Continuous cornfields were positively correlated with abundance of *D. barberi*, but abundance negatively correlated with the number of years corn was continuously planted in a field. Multiple regression analysis of field history data explained 54% of the variation in the ratio of *D. v. virgifera* to *D. barberi* and both current problem fields and years planted to corn continuously were significantly and positively correlated with the ratio of *D. v. virgifera* to *D. barberi* (Table 3).

Significant differences among field types were present for field histories (Table 4). The proportion of years planted to corn between 2003 and the year fields were sampled was significantly lower for recently rotated fields compared the other field types. Crop rotations in recently rotated fields varied in length from three-year rotation schemes with one year planted to a non-corn crop (i.e., two years of corn followed by soybean (*Glycine max* L.)) to seven-year rotation with five consecutive years of non-corn crops (i.e., corn planted for two years, alfalfa *Medicago sativa* L. planted for four years and one year of oats *Avena sativa* L.) (Supp. Table S1). Soybean was only other crop planted in all continuous cornfields and past problem fields and was the only other crop in seven of the nine current problem fields (Supp. Tables S2, S3 and S4). The proportion of years planted to corn continuously was significantly lower in recently rotated fields, which was expected given the criteria for selecting those fields, but did not differ among continuous cornfields, past problem fields and current problem fields (Table 4).

Management of *Diabrotica* spp. differed significantly among field types. The use of non-Bt corn differed significantly among field types with recently rotated fields planted to non-Bt corn more often than past problem fields, which were almost never planted to non-Bt corn (Table 4). Furthermore, when fields were planted to corn, significantly more Cry3Bb1 corn was planted in past problem fields compared to Cry3Bb1 corn planted in recently rotated fields (Table 4). Continuous cornfields and current problem fields did not differ from any other field type in either the planting of non-Bt corn or Cry3Bb1 corn. Planting of Cry34/35Ab1, mCry3A, or Cry3Bb1 and Cry34/35Ab1 pyramided corn did not differ among field types (Table 4). No fields sampled contained corn producing eCry3.1Ab toxin. Use of soil-applied insecticide also differed significantly among field types (Table 4), and was significantly lower in recently rotated fields and current problem fields compared to continuous cornfields. Use of foliar insecticides on corn was very rare, and did not differ among field types (Table 4).

Field histories of past problem fields differed significant between the time before and after greater than expected injury to Bt corn was observed (Table 5). The use of Cry3Bb1 corn in past problem fields was significantly higher before versus after the observation of greater than expected injury. The amount of corn planted continuously in past problem fields was significantly greater after versus before severe injury to Bt corn was observed. Additionally after greater than expected injury, farmers planted more pyramided Cry3Bb1 and Cry34/35Ab1 corn and applied soil insecticide more often.

Discussion

We sampled 47 cornfields in Iowa during 2013 and 2014 and found significantly greater root injury (Fig. 2) and abundance of *D. v. virgifera* (Fig. 3) in current problem fields

compared to recently rotated fields, continuous cornfields and past problem fields. Although root injury, abundance of *D. v. virgifera* and abundance of *D. barberi* (Fig. 4) did not differ among recently rotated fields, continuous cornfields and past problem fields, inputs for management of *Diabrotica* spp. in recently rotated fields were significantly lower in terms of the amount of Cry3Bb1 corn planted and the application of a soil insecticide (Table 4). Additionally, field histories were similar between continuous cornfields and current problem fields with the exception of significantly greater use of soil applied insecticides in continuous cornfields. This result implies that the addition of soil applied insecticides may have prevented continuous cornfields from becoming current problem fields. In past problem fields, farmers mitigated the risk of injury from potentially Bt-resistant *D. v. virgifera* populations by planting more pyramided Bt corn and increasing the use of soil applied insecticides (Table 5).

Previous studies have characterized root injury from cornfields with unexpected injury to Bt corn (Gassmann et al. 2011, 2012, 2014; Wangila et al. 2015), which were similar to the level of root injury observed here in current problem fields (Fig. 2). We additionally sampled adult *D. v. virgifera* and *D. barberi* from current problem fields and found that peak abundance of *D. v. virgifera* alone exceeded the traditional economic threshold of 6 *Diabrotica* spp. captured per sticky trap per day (Hein and Tollefson 1985) on average by 5 fold and 4 fold during 2013 and 2014, respectfully (Fig. 3). Again, similar to other studies (Gassmann et al. 2011, 2012, 2014; Wangila et al. 2015), field histories from current problem fields illustrated a pattern of relying primarily on Cry3Bb1 corn for management of *Diabrotica* spp., with no applications of conventional insecticides and low instances of crop rotation (Table 4, Supp. Table S4). Laboratory strains of *D. v. virgifera*

have been selected for resistance to Cry3Bb1 corn, and resistance can develop in as few as three generations of selection (Meihls et al. 2008). Other laboratory strains of *D. v. virgifera* have also been selected for resistance to Cry34/35Ab1 (Lefko et al. 2008, Deitloff et al. 2015), mCry3A (Meihls et al. 2011) and eCry3.1Ab (Frank et al. 2013) Bt toxins, and resistance also developed rapidly. Although populations of *D. v. virgifera* from currently problem fields were not screened for Bt resistance as part of this study, considering the evidence that Bt resistance can be rapidly selected and the similarity in field history with previously sampled fields with Bt-resistant populations suggests that *D. v. virgifera* from currently problem fields may have been Bt resistant.

We hypothesized that, following greater than expected injury to Cry3 corn, farmers might mitigate the risk of future root injury by either rotating fields out of corn production, changing the type of Bt corn planted, applying more conventional insecticides or some combination of these approaches. We found that farmers of past problem fields grew significantly more continuous corn after experiencing greater than expected injury to Cry3 corn, indicating that increased crop rotation was not used to mitigate the risk of future *Diabrotica* spp. injury. However, following greater than expected injury farmer grew significantly more corn pyramided with Cry3Bb1 and Cry34/35Ab1, applied soil-insecticides more frequently and grew Cry3Bb1 corn significantly less (Table 5). These data indicate that farmers have typically mitigated instances of greater than expected injury to Bt corn by primarily growing corn pyramided with Cry3Bb1 and Cry34/35Ab1 either alone or with soil-applied insecticide.

Field histories were similar among continuous cornfields and current problem fields (Table 4, Supp. Tables S2 and S4), with the exception of soil applied insecticide use in

continuous cornfields. This difference suggests that soil-applied insecticides may have been an important factor in preventing the occurrence of greater than expected injury to Bt corn. However, this does not mean that *D. v. virgifera* in continuous cornfields are susceptible to Cry3Bb1 corn. Pyramids are effective at delaying resistance when toxins in the pyramid have independent modes of action and mortality is high for homozygous susceptible individuals, but pyramids become less effective at delaying resistance as pest mortality decreases (Comins 1986, Gould 1998, Roush 1998, Tabashnik and Gould 2012). Pyramiding soil applied insecticides with Bt corn may be detrimental for resistance management of *Diabrotica* spp. because soil insecticides typically do not kill enough larvae to delay resistance to Bt corn (Petzold-Maxwell et al. 2013). Furthermore, field experiments have demonstrated that combining soil applied insecticide with Bt corn delays adult emergence (Petzold-Maxwell et al. 2013), which can promote assortative mating of Bt-selected individuals leading to more rapid Bt resistance evolution (Gould 1998). While use of insecticides may have reduced the risk of greater than expected injury, it is currently unknown to what extent insecticides effect on the rate of resistance development.

Incorporating IPM with multiple tactics can suppress populations of *Diabrotica* spp. and may increase the durability of Bt corn (Gassmann 2012, Tabashnik and Gould 2012). Additionally, IPM can reduce the need for farmers to invest in pest management inputs. Root injury and the abundance of *D. v. virgifera* did not differ among recently rotated fields, continuous cornfields and past problem fields, however recently rotated fields planted significantly less Bt corn and used significantly less soil applied insecticide (Table 4). Furthermore, IPM can complement resistance management by diversifying the causes of pest morality (McGaughey and Whalon 1992). Although increasing the use of crop rotation

would diversify the causes of *Diabrotica* spp. morality compared to only relying on Bt corn, incorporating crop rotation alone may not be the optimal strategy for delaying Bt resistance. There are areas of the Corn Belt where both Bt-resistant and rotation-resistant *D. v. virgifera* already co-occur (Gray et al. 2009, Gray 2014). Models analyzing the predicted interactions among Bt resistance, rotation resistance and *D. v. virgifera* indicate that in areas where rotation resistance is absent, like Iowa (Dunbar and Gassmann 2013), inheritance of Bt resistance is the most important factor affecting the development of Bt resistance, regardless of the area planted to continuous corn (Crowder et al. 2005). Where rotation-resistant *D. v. virgifera* is present or thought to soon become an issue, planting first-year corn that produce Bt toxins can delay resistance to both Bt corn and crop rotation (Crowder et al. 2005). Additional key components of IPM include the use of economic thresholds and scouting to determine the need for pest management (Pedigo and Rice 2006). Although adult abundance on average exceeded the economic threshold in all field types, some individual fields had peak abundances below economic thresholds suggesting that management of *Diabrotica* spp. would not be needed in those fields if planted to corn the following year. However, it is difficult to predict larval injury based on adult abundance, which means economic thresholds for *Diabrotica* spp. may be of limited value (Foster et al. 1986) and a survey of Iowa farmers has shown that less than half scout for adult *Diabrotica* spp. (Arbuckle 2013).

Competition among closely related species that occupy similar ecological niches can result in species displacement (Reitz and Trumble 2002). Evidence for competition was observed in previously sampled Iowa cornfields that were dominated by either *D. barberi* or *D. v. virgifera* (Dunbar and Gassmann 2013). Although both *D. barberi* and *D. v. virgifera* were captured by sticky traps from all 47 cornfields in this study, the average ratio of *D. v.*

virgifera to *D. barberi* in recently rotated cornfields was lower compared to the other field types, especially compared to currently problem fields (Table 2). There are two factors that may explain these observations. The first is that Iowa has rotation-resistant *D. barberi* but not rotation-resistant *D. v. virgifera* (Levine and Oloumi-Sadeghi 1991, Dunbar and Gassmann 2013). Previous studies conducted in other areas of the Corn Belt with rotation-resistant *D. barberi*, but without rotation-resistant *D. v. virgifera*, have documented greater prevalence of *D. barberi* in areas where there is a greater frequency of crop rotation (Hill and Mayo 1980). Secondly, *D. barberi* is an inferior competitor to *D. v. virgifera*. Greenhouse studies of intraspecific and interspecific competition among varying infestations rates of each species have shown that *D. v. virgifera* survival is affected more by intraspecific competition and *D. barberi* survival is affected by both intraspecific and interspecific competition (Piedrahita et al. 1985, Woodson 1993, 1994). In landscapes dominated by continuous cornfields *D. v. virgifera* have been observed to displace *D. barberi* (Hill and Mayo 1980). *Diabrotica* spp. populations in current problem fields were composed predominantly of *D. v. virgifera*. This likely arose because Bt resistance permitted the survival of *D. v. virgifera,* and as populations of *D. v. virgifera* increased, displaced *D. barberi* as they could not compete.

Diversifying management of *Diabrotica* spp. by incorporating IPM tactics such as crop rotation with the judicious use Bt corn and conventional insecticides may decrease yield loss from *Diabrotica* spp. and help to delay the evolution of resistance. Data presented here showed that low root injury and low abundance of adult *Diabrotica* spp. were present in recently rotated fields, and that recently rotated fields required significantly fewer management inputs compared to continuous cornfields and past problem fields. Furthermore, severe root injury and large populations of *D. v. virgifera* were associated with fields that

lacked management diversity. As with many pest species, utilizing a diverse set of pest management practices likely offers the most sustainable approach for management of *Diabrotica* spp.

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Tables

Table 1. *Diabrotica* spp. management by field type in 2013 and 2014

		# Fields (# Fields with Soil Insecticide)				
Field Types[1]	**N**	**Non-Bt**	**Cry3Bb1**	**Cry34/35Ab1**	**mCry3A**	**Cry3Bb1 + Cry34/35Ab1**
2013						
Recently Rotated Field	5	1 (1)	0 (0)	2 (0)	1 (0)	1 (0)
Continuous Cornfield	5	1 (1)	1 (1)	3 (1)	0 (0)	0 (0)
Past Problem Field	5	0 (0)	0 (0)	0 (0)	0 (0)	5 (2)
Current Problem Field	5	0 (0)	5 (0)	0 (0)	0 (0)	0 (0)
2014						
Recently Rotated Field	7	1 (0)	0 (0)	2 (0)	0 (0)	4 (0)
Continuous Cornfield	8	1 (0)	1 (1)	0 (0)	0 (0)	6 (1)
Past Problem Field	8	1 (0)	1 (1)	0 (0)	0 (0)	6 (3)
Current Problem Field	4	0 (0)	2 (0)	0 (0)	2 (0)	0 (0)

[1] Field types sampled in 2013 and 2014: Recently Rotated Field = 2nd year cornfields, Continuous Cornfield= fields planted continuously to corn for > 7 years, Past Problem Field = cornfields with a history of greater than expected injury (> 1 node injured) to Bt corn, Current Problem Field = cornfields currently experiencing greater than 1 root node of injury to Bt corn during the year sampled.

Table 2. Ratio of *Diabrotica v. virgifera* to *D. barberi* captured by sticky traps by field type in 2013 and 2014

Field Types[1]	Ratio *D. v. virgifera* to *D. barberi* 2013[2]	2014
Recently Rotated Field	10.6 ± 7.3b	0.9 ± 0.4b
Continuous Cornfield	16.2 ± 6.0b	11.9 ± 6.3ab
Past Problem Field	57.7 ± 30.2b	9.3 ± 4.6ab
Current Problem Field	1,562.3 ± 859.9a	26.1 ± 12.6a

[1] Field types sampled in 2013 and 2014: Recently Rotated Field = 2nd year cornfields, Continuous Cornfield= fields planted continuously to corn for > 7 years, Past Problem Field = cornfields with a history of greater than expected injury (> 1 node injured) to Bt corn, Current Problem Field = cornfields currently experiencing greater than 1 root node of injury to Bt corn during the year sampled.

[2] Letters denote significant differences among field types within year sampled.

Table 3. Multiple linear regression for root injury, abundance of *D. v. virgifera*, abundance of *D. barberi* and the ratio of *D. v. virgifera* to *D. barberi*

Dependent Variable	Parameters	Slope	SE	*F*	*P*	Model r^2
Root Injury						0.59
	Current Problem Fields	1.125	0.229	24.46	<0.0001	
	(Intercept)	-0.855	0.142	36.33	<0.0001	
Abundance of *D.v.v.*						0.51
	Current Problem Fields	1.543	0.278	30.70	<0.0001	
	Planted to Cry34/35Ab1 Corn during year sampled	0.842	0.319	6.98	0.013	
	(Intercept)	-0.059	0.132	0.20	0.66	
Abundance of *D.b.*						0.44
	Continuous Cornfields	0.545	0.197	7.62	0.010	
	Years of Continuous Corn	-1.238	0.279	19.65	0.0001	
	(Intercept)	-0.052	0.164	0.10	0.75	
Ratio of *D.v.v.* to *D.b.*						0.54
	Current Problem Fields	1.473	0.332	19.66	0.0001	
	Years of Continuous Corn	1.394	0.441	9.98	0.003	
	(Intercept)	-0.089	0.258	0.12	0.73	

Table 4. Analysis of variance among field types for various management approaches and cropping history

				Field Types[2, 3]			
Cropping History Factor[1]	***F***	**df**	***P***	**Rotated**	**Continuous**	**Past Problem**	**Current Problem**
Planted to Corn	19.22	3, 33	<0.0001	0.49 ± 0.05b	0.94 ± 0.02a	0.87 ± 0.04a	0.77 ± 0.08a
Planted to Continuous Corn	14.18	3, 33	<0.0001	0.17 ± 0.01b	0.84 ± 0.06a	0.66 ± 0.09a	0.55 ± 0.13a
Planted to Non-Bt Corn	4.31	3, 33	0.011	0.61 ± 0.12a	0.30 ± 0.11ab	0.10 ± 0.06b	0.34 ± 0.11ab
Cry3Bb1 Corn	4.58	3, 33	0.009	0.22 ± 0.11b	0.45 ± 0.12ab	0.73 ± 0.07a	0.60 ± 0.12ab
Cry34/35Ab1 Corn	2.66	3, 33	0.06	0.05 ± 0.03	0.13 ± 0.06	0.00 ± 0.00	0.00 ± 0.00
mCry3A Corn	1.09	3, 33	0.37	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.01	0.03 ± 0.03
Cry3Bb1 + Cry34/35Ab1 Corn	1.91	3, 33	0.15	0.13 ± 0.05	0.12 ± 0.04	0.17 ± 0.03	0.03 ± 0.02
Soil Insecticide Applied	4.59	3, 33	0.009	0.02 ± 0.02c	0.31 ± 0.10ab	0.14 ± 0.05bc	0.00 ± 0.00c
Foliar Insecticide Applied	2.35	3, 33	0.09	0.00 ± 0.00	0.06 ± 0.02	0.03 ± 0.02	0.00 ± 0.00

[1] Data presented on the proportion of total years each management approach was used in a field, with data presented as mean ± standard error of the mean.

[2] Field types sampled in 2013 and 2014: Recently Rotated Field = 2nd year cornfields, Continuous Cornfield= fields planted continuously to corn for > 7 years, Past Problem Field = cornfields with a history of greater than expected injury (> 1 node injured) to Bt corn, Current Problem Field = cornfields currently experiencing greater than 1 root node of injury to Bt corn during the year sampled.

[3] Letters denote significant differences among field types within year sampled.

Table 5. Paired *t*-test comparing management approaches in fields before and after greater than expected injury to Bt corn

				Past Problem Fields[1]	
Cropping History Factor	***T***	**df**	***P***	**Before Injury**	**After Injury**
Planted to Corn	2.14	9	0.06	0.86 ± 0.05	0.98 ± 0.02
Planted to Continuous Corn	2.93	9	0.017	0.66 ± 0.10	0.98 ± 0.02
Planted to Non-Bt Corn	1.50	9	0.17	0.11 ± 0.08	0.00 ± 0.00
Cry3Bb1 Corn	5.33	9	0.0005	0.87 ± 0.07	0.25 ± 0.12
Cry34/35Ab1 Corn	.	.	.	0.00 ± 0.00	0.00 ± 0.00
mCry3A Corn	1.00	9	0.34	0.00 ± 0.00	0.01 ± 0.01
Cry3Bb1 + Cry34/35Ab1 Corn	6.55	9	0.0001	0.00 ± 0.00	0.75 ± 0.12
Soil Insecticide Applied	2.77	9	0.022	0.03 ± 0.02	0.36 ± 0.12
Foliar Insecticide Applied	0.50	9	0.63	0.03 ± 0.02	0.05 ± 0.05

[1] Data presented on the proportion of total years each management approach was used in a field, with data presented as mean ± standard error of the mean.

Figures

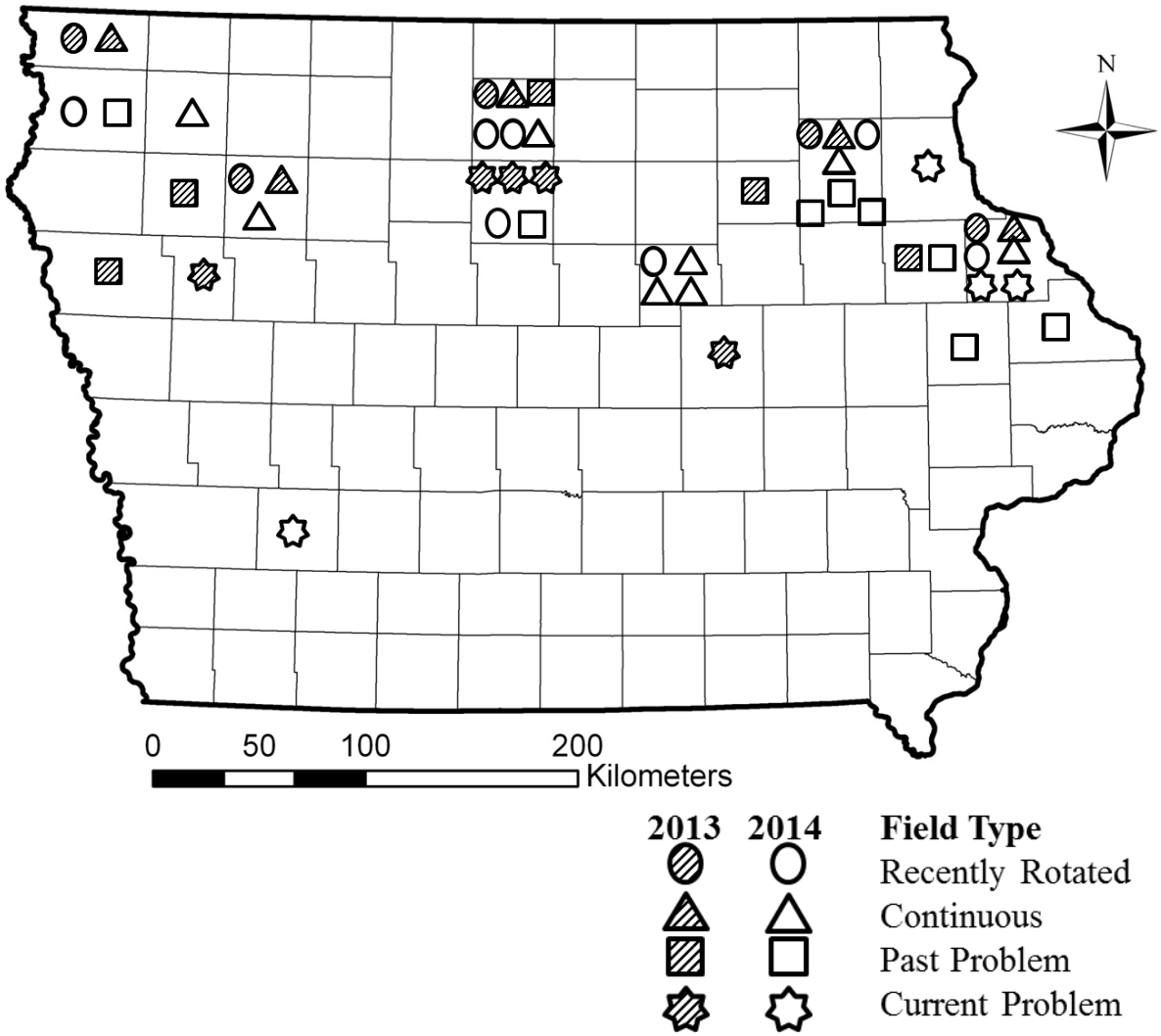

Figure 1. Distribution of cornfields sampled in 2013 and 2014. Location of each field is accurate to the level of county.

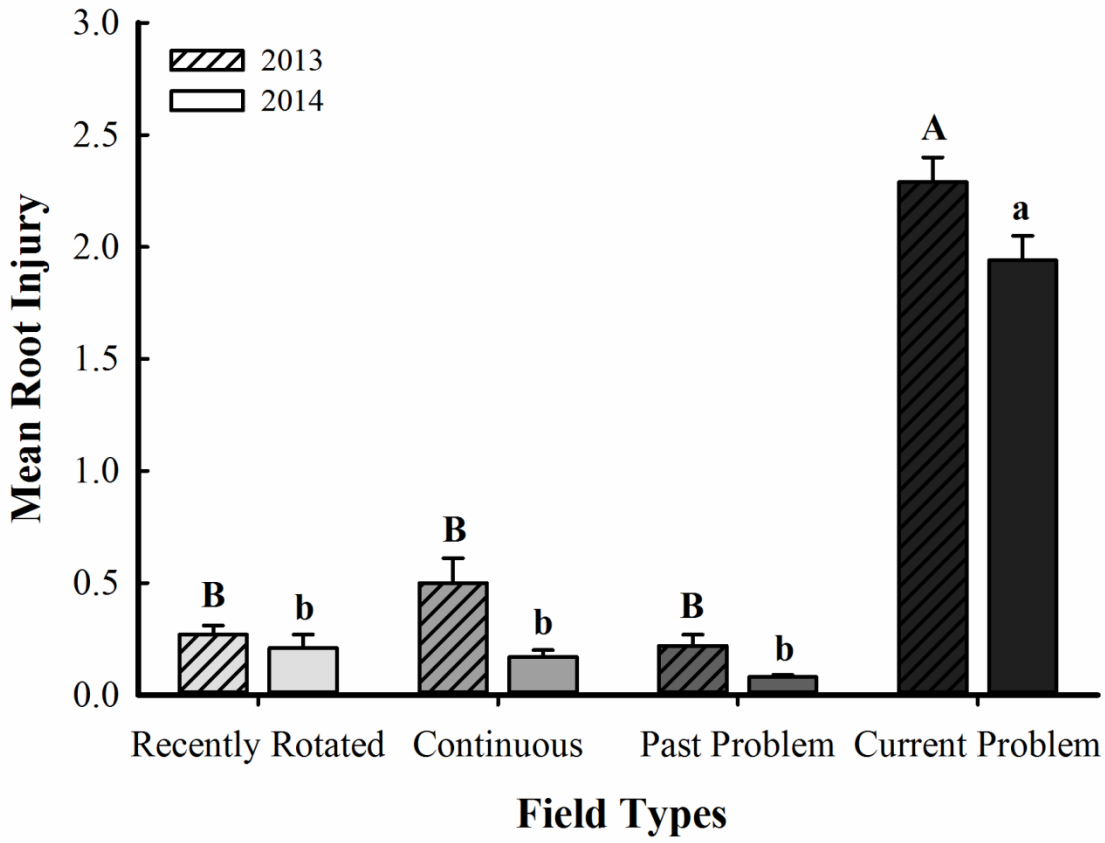

Figure 2. Root injury by field type for 2013 and 2014. Root injury was scored on the 0 to 3 node-injury scale (Oleson et al. 2005). Bar heights represent sample means and error bars are the standard error of the mean. Capital letters denote significant differences among field types in 2013 and low case letters represent significant differences among field types in 2014.

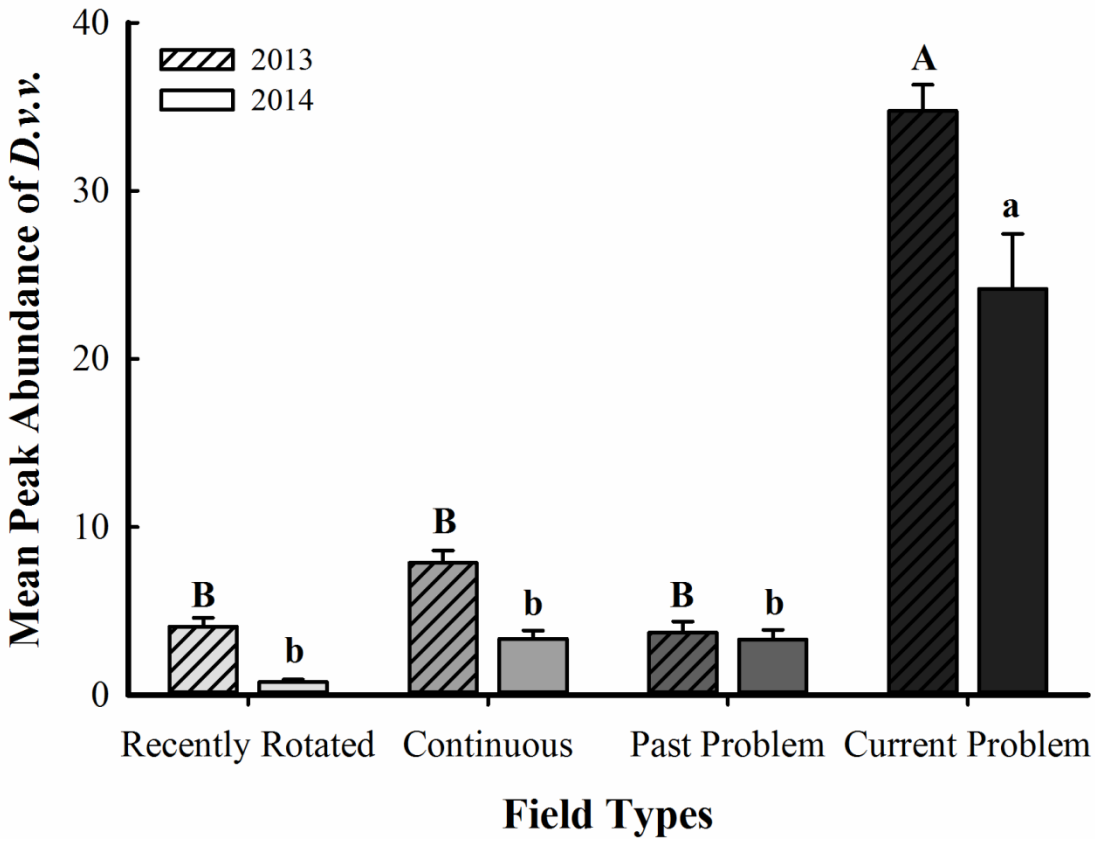

Figure 3. Mean peak abundance *Diabrotica virgifera virgifera* by field type for 2013 and 2014. Bar heights represent sample means and error bars are the standard error of the mean. Capital letters denote significant differences among field types in 2013 and low case letters represent significant differences among field types in 2014.

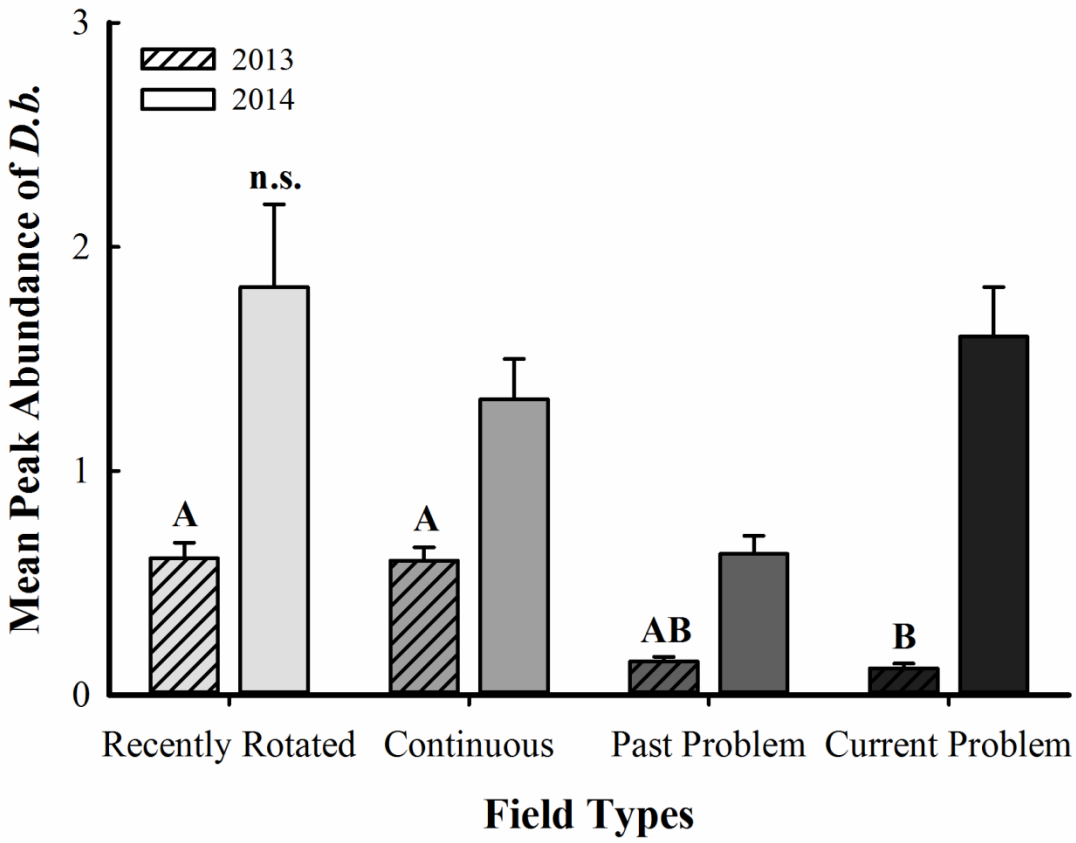

Figure 4. Mean peak abundance *Diabrotica barberi* by field type for 2013 and 2014. Bar heights represent sample means and error bars are the standard error of the mean. Capital letters denote significant differences among field types in 2013.

Supplemental Tables

Supplemental Table S1. Field history of recently rotated fields sampled in 2013 and 2014

Year	Sampled Field #	2014 1	2014 2	2014 3	2014 4	2014 5	2014 6[5]	2014 7[5]
2014	**Crop**[1]	Corn	Corn	Corn	Corn	Corn	Corn	Corn
	Bt Toxin[2]	0	4	4	4	4	2	2
	Soil[3]	None	None	None	None	None	None	None
	Foliar[4]	None	None	None	None	None	None	None
2013	**Crop**	Corn	Corn	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	0	0	1	0	Uk	Uk	Uk
	Soil	None	None	None	None	Uk	Uk	Uk
	Foliar	None	None	None	None	Uk	Uk	Uk
2012	**Crop**	Alfa	Alfa	Soy	Soy	Alfa	Soy	Soy
	Bt Toxin	.	.	.	.	.	.	.
	Soil	.	.	.	.	.	.	.
	Foliar	.	.	.	.	.	.	.
2011	**Crop**	Alfa	Alfa	Corn	Corn	Alfa	Corn	Corn
	Bt Toxin	.	.	1	1	.	Uk	Uk
	Soil	.	.	None	None	.	Uk	Uk
	Foliar	.	.	None	None	.	Uk	Uk
2010	**Crop**	Alfa	Alfa	Soy	Corn	Alfa	Soy	Soy
	Bt Toxin	.	.	.	0	.	.	.
	Soil	.	.	.	None	.	.	.
	Foliar	.	.	.	None	.	.	.
2009	**Crop**	Oats	Oats	Corn	Soy	Alfa	Corn	Corn
	Bt Toxin	.	.	1	.	.	Uk	Uk
	Soil	.	.	None	.	.	Uk	Uk
	Foliar	.	.	None	.	.	Uk	Uk
2008	**Crop**	Corn	Corn	Soy	Corn	Oats	Soy	Corn
	Bt Toxin	0	0	.	1	.	.	Uk
	Soil	None	None	.	None	.	.	Uk
	Foliar	None	None	.	None	.	.	Uk

[1] Crop planted: Corn = Corn, Soy = Soybean; Oats = Oats; Alfa = Alfalfa; Sod = Sod, Uk = unknown.

[2] Rootworm active Bt corn: 0 = no rootworm active Bt, 1 = Cry3Bb1, 2 = Cry34/35Ab1, 3 = mCry3A, 4 = Cry3Bb1 & Cry34/35Ab1, Uk = unknown.

[3] Soil applied insecticide used, Uk = unknown.

[4] Foliar applied insecticide used, Uk = unknown.

[5] Field excluded from cropping history analyses.

Supplemental Table S1 Continued. Field history of recently rotated fields sampled in 2013 and 2014

Year	Sampled Field #	2014 1	2014 2	2014 3	2014 4	2014 5	2014 6[5]	2014 7[5]
2007	**Crop**[1]	Corn	Corn	Corn	Corn	Corn	Corn	Corn
	Bt Toxin[2]	0	0	1	0	0	Uk	Uk
	Soil[3]	None	None	None	None	None	Uk	Uk
	Foliar[4]	None	None	None	None	None	Uk	Uk
2006	**Crop**	Alfa	Alfa	Soy	Soy	Corn	Soy	Soy
	Bt Toxin	.	.	.	.	Uk	.	.
	Soil	.	.	.	.	Uk	.	.
	Foliar	.	.	.	.	Uk	.	.
2005	**Crop**	Alfa	Alfa	Corn	Corn	Soy	Corn	Corn
	Bt Toxin	.	.	1	1	.	Uk	Uk
	Soil	.	.	None	None	.	Uk	Uk
	Foliar	.	.	None	None	.	Uk	Uk
2004	**Crop**	Alfa	Alfa	Soy	Corn	Corn	Soy	Soy
	Bt Toxin	.	.	.	0	Uk	.	.
	Soil	.	.	.	None	Uk	.	.
	Foliar	.	.	.	None	Uk	.	.
2003	**Crop**	Oats	Oats	Corn	Soy	Alfa	Corn	Corn
	Bt Toxin	.	.	1	.	.	Uk	Uk
	Soil	.	.	None	.	.	Uk	Uk
	Foliar	.	.	None	.	.	Uk	Uk

[1] Crop planted: Corn = Corn, Soy = Soybean; Oats = Oats; Alfa = Alfalfa; Sod = Sod, Uk = unknown.

[2] Rootworm active Bt corn: 0 = no rootworm active Bt, 1 = Cry3Bb1, 2 = Cry34/35Ab1, 3 = mCry3A, 4 = Cry3Bb1 & Cry34/35Ab1, Uk = unknown.

[3] Soil applied insecticide used, Uk = unknown.

[4] Foliar applied insecticide used, Uk = unknown.

[5] Field excluded from cropping history analyses.

Supplemental Table S1 Continued. Field history of recently rotated fields sampled in 2013 and 2014

Year	Sampled Field #	2013 8	2013 9[5]	2013 10	2013 11	2013 12
2014	**Crop**[1]	.	.	.	.	.
	Bt Toxin[2]	.	.	.	.	.
	Soil[3]	.	.	.	.	.
	Foliar[4]	.	.	.	.	.
2013	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	0	3	4	2	2
	Soil	Yes	None	None	None	None
	Foliar	None	None	None	None	None
2012	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	0	Uk	4	0	0
	Soil	None	Uk	None	None	None
	Foliar	None	Uk	None	None	None
2011	**Crop**	Soy	Soy	Soy	Alfa	Alfa
	Bt Toxin	.	.	.	.	.
	Soil	.	.	.	.	.
	Foliar	.	.	.	.	.
2010	**Crop**	Corn	Corn	Corn	Alfa	Alfa
	Bt Toxin	1	Uk	4	.	.
	Soil	None	Uk	None	.	.
	Foliar	None	Uk	None	.	.
2009	**Crop**	Soy	Soy	Soy	Alfa	Alfa
	Bt Toxin	.	.	.	.	.
	Soil	.	.	.	.	.
	Foliar	.	.	.	.	.
2008	**Crop**	Corn	Corn	Corn	Oats	Alfa
	Bt Toxin	0	Uk	1	.	.
	Soil	None	Uk	None	.	.
	Foliar	None	Uk	None	.	.

[1] Crop planted: Corn = Corn, Soy = Soybean; Oats = Oats; Alfa = Alfalfa; Sod = Sod, Uk = unknown.

[2] Rootworm active Bt corn: 0 = no rootworm active Bt, 1 = Cry3Bb1, 2 = Cry34/35Ab1, 3 = mCry3A, 4 = Cry3Bb1 & Cry34/35Ab1, Uk = unknown.

[3] Soil applied insecticide used, Uk = unknown.

[4] Foliar applied insecticide used, Uk = unknown.

[5] Field excluded from cropping history analyses.

Supplemental Table S1 Continued. Field history of recently rotated fields sampled in 2013 and 2014

Year	Sampled Field #	2013 8	2013 9[5]	2013 10	2013 11	2013 12
2007	**Crop**[1]	Soy	Soy	Corn	Corn	Oats
	Bt Toxin[2]	.	.	Uk	0	.
	Soil[3]	.	.	Uk	None	.
	Foliar[4]	.	.	Uk	None	.
2006	**Crop**	Corn	Corn	Soy	Soy	Corn
	Bt Toxin	0	Uk	.	.	0
	Soil	None	Uk	.	.	None
	Foliar	None	Uk	.	.	None
2005	**Crop**	Soy	Corn	Corn	Corn	Corn
	Bt Toxin	.	Uk	1	0	0
	Soil	.	Uk	None	None	None
	Foliar	.	Uk	None	None	None
2004	**Crop**	Corn	Corn	Soy	Soy	Alfa
	Bt Toxin	Uk	Uk	.	.	.
	Soil	Uk	Uk	.	.	.
	Foliar	Uk	Uk	.	.	.
2003	**Crop**	Corn	Soy	Corn	Corn	Alfa
	Bt Toxin	Uk	.	1	0	.
	Soil	Uk	.	None	None	.
	Foliar	Uk	.	None	None	.

[1] Crop planted: Corn = Corn, Soy = Soybean; Oats = Oats; Alfa = Alfalfa; Sod = Sod, Uk = unknown.

[2] Rootworm active Bt corn: 0 = no rootworm active Bt, 1 = Cry3Bb1, 2 = Cry34/35Ab1, 3 = mCry3A, 4 = Cry3Bb1 & Cry34/35Ab1, Uk = unknown.

[3] Soil applied insecticide used, Uk = unknown.

[4] Foliar applied insecticide used, Uk = unknown.

[5] Field excluded from cropping history analyses.

Supplemental Table S2. Field history of continuous cornfields sampled in 2013 and 2014

Year	Sampled Field #	2014 1	2014 2	2014 3	2014 4	2014 5	2014 6	2014 7[5]	2014 8[5]
2014	**Crop**[1]	Corn	Corn	Corn	Corn	Corn	Corn	Corn	Corn
	Bt Toxin[2]	1	4	4	4	4	4	4	0
	Soil[3]	Yes	None	Yes	None	None	None	None	Uk
	Foliar[4]	Yes	None	None	None	None	None	None	Uk
2013	**Crop**	Corn	Corn	Corn	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	2	2	4	2	4	4	Uk	Uk
	Soil	None	None	Yes	None	None	None	Uk	Uk
	Foliar	None	None	None	None	None	None	Uk	Uk
2012	**Crop**	Corn	Corn	Corn	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	None	1	4	1	0	0	Uk	Uk
	Soil	Yes	Yes	None	None	Yes	Yes	Uk	Uk
	Foliar	None	Yes	Yes	None	None	None	Uk	Uk
2011	**Crop**	Corn	Corn	Corn	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	1	2	4	1	0	0	Uk	Uk
	Soil	None	None	None	None	Yes	Yes	Uk	Uk
	Foliar	None	None	None	None	None	None	Uk	Uk
2010	**Crop**	Corn	Corn	Corn	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	2	Yes	4	1	0	0	Uk	Uk
	Soil	None	Yes	None	None	Yes	Yes	Uk	Uk
	Foliar	None	Yes	None	None	None	None	Uk	Uk
2009	**Crop**	Corn	Corn	Corn	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	None	2	1	1	0	0	Uk	Uk
	Soil	None	None	None	None	Yes	Yes	Uk	Uk
	Foliar	None	None	None	None	None	None	Uk	Uk
2008	**Crop**	Corn	Corn	Corn	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	1	None	1	1	0	0	Uk	Uk
	Soil	None	None	None	None	Yes	Yes	Uk	Uk
	Foliar	None	None	None	None	None	None	Uk	Uk

[1] Crop planted: Corn = Corn, Soy = Soybean; Oats = Oats; Alfa = Alfalfa; Sod = Sod, Uk = unknown.

[2] Rootworm active Bt corn: 0 = no rootworm active Bt, 1 = Cry3Bb1, 2 = Cry34/35Ab1, 3 = mCry3A, 4 = Cry3Bb1 & Cry34/35Ab1, Uk = unknown.

[3] Soil applied insecticide used, Uk = unknown.

[4] Foliar applied insecticide used, Uk = unknown.

[5] Field excluded from cropping history analyses.

Supplemental Table S2 Continued. Field history of continuous cornfields sampled in 2013 and 2014

Year	Sampled Field #	2014 1	2014 2	2014 3	2014 4	2014 5	2014 6	2014 7[5]	2014 8[5]
2007	**Crop**[1]	Soy	Soy	Corn	Corn	Corn	Corn	Soy	Corn
	Bt Toxin[2]	.	.	1	1	0	0	.	Uk
	Soil[3]	.	.	None	None	Yes	Yes	.	Uk
	Foliar[4]	.	.	None	None	None	None	.	Uk
2006	**Crop**	Corn	Corn	Corn	Corn	Corn	Corn	Corn	Soy
	Bt Toxin	1	Uk	1	1	0	0	Uk	.
	Soil	None	Uk	None	None	Yes	Yes	Uk	.
	Foliar	None	Uk	None	None	None	None	Uk	.
2005	**Crop**	Corn	Soy	Soy	Corn	Corn	Corn	Soy	Corn
	Bt Toxin	1	.	.	1	0	0	.	Uk
	Soil	None	.	.	None	Yes	Yes	.	Uk
	Foliar	None	.	.	None	None	None	.	Uk
2004	**Crop**	Corn	Corn	Corn	Corn	Corn	Corn	Corn	Soy
	Bt Toxin	1	Uk	1	1	0	0	Uk	.
	Soil	None	Uk	None	None	Yes	Yes	Uk	.
	Foliar	None	Uk	None	None	None	None	Uk	.
2003	**Crop**	Corn	Soy	Corn	Corn	Corn	Corn	Soy	Corn
	Bt Toxin	1	.	1	1	0	0	.	Uk
	Soil	None	.	None	None	Yes	Yes	.	Uk
	Foliar	None	.	None	None	None	None	.	Uk

[1] Crop planted: Corn = Corn, Soy = Soybean; Oats = Oats; Alfa = Alfalfa; Sod = Sod, Uk = unknown.

[2] Rootworm active Bt corn: 0 = no rootworm active Bt, 1 = Cry3Bb1, 2 = Cry34/35Ab1, 3 = mCry3A, 4 = Cry3Bb1 & Cry34/35Ab1, Uk = unknown.

[3] Soil applied insecticide used, Uk = unknown.

[4] Foliar applied insecticide used, Uk = unknown.

[5] Field excluded from cropping history analyses.

Supplemental Table S2 Continued. Field history of continuous cornfields sampled in 2013 and 2014

Year	Sampled Field #	2013 9	2013 10	2013 11	2013 12	2013 13
2014	**Crop**[1]	.	.	.	.	.
	Bt Toxin[2]	.	.	.	.	.
	Soil[3]	.	.	.	.	.
	Foliar[4]	.	.	.	.	.
2013	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	2	0	1	2	2
	Soil	Yes	Yes	Yes	None	None
	Foliar	None	None	None	None	None
2012	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	None	4	1	4	1
	Soil	Yes	None	None	None	None
	Foliar	None	Yes	Yes	None	None
2011	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	0	4	1	2	1
	Soil	Yes	None	None	None	None
	Foliar	None	None	None	None	None
2010	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	0	1	1	1	1
	Soil	None	None	None	None	None
	Foliar	None	None	None	None	None
2009	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	1	1	1	2	1
	Soil	None	None	None	None	None
	Foliar	None	None	None	None	None
2008	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	0	1	1	2	1
	Soil	Yes	None	None	None	None
	Foliar	None	None	None	None	None

[1] Crop planted: Corn = Corn, Soy = Soybean; Oats = Oats; Alfa = Alfalfa; Sod = Sod, Uk = unknown.

[2] Rootworm active Bt corn: 0 = no rootworm active Bt, 1 = Cry3Bb1, 2 = Cry34/35Ab1, 3 = mCry3A, 4 = Cry3Bb1 & Cry34/35Ab1, Uk = unknown.

[3] Soil applied insecticide used, Uk = unknown.

[4] Foliar applied insecticide used, Uk = unknown.

[5] Field excluded from cropping history analyses.

Supplemental Table S2 Continued. Field history of continuous cornfields sampled in 2013 and 2014

Year	Sampled Field #	2013 9	2013 10	2013 11	2013 12	2013 13
2007	**Crop**[1]	Corn	Corn	Corn	Corn	Corn
	Bt Toxin[2]	0	1	1	2	1
	Soil[3]	Yes	None	None	None	None
	Foliar[4]	None	None	None	None	None
2006	**Crop**	Corn	Soy	Corn	Corn	Corn
	Bt Toxin	0	.	1	2	1
	Soil	Yes	.	None	None	None
	Foliar	None	.	None	None	None
2005	**Crop**	Corn	Corn	Soy	Corn	Corn
	Bt Toxin	0	1	.	0	1
	Soil	Yes	None	.	Yes	None
	Foliar	None	None	.	None	None
2004	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	Uk	1	1	0	1
	Soil	Uk	None	None	None	None
	Foliar	Uk	None	None	None	None
2003	**Crop**	Corn	Corn	Corn	Soy	Corn
	Bt Toxin	Uk	1	1	.	1
	Soil	Uk	None	None	.	None
	Foliar	Uk	None	None	.	None

[1] Crop planted: Corn = Corn, Soy = Soybean; Oats = Oats; Alfa = Alfalfa; Sod = Sod, Uk = unknown.

[2] Rootworm active Bt corn: 0 = no rootworm active Bt, 1 = Cry3Bb1, 2 = Cry34/35Ab1, 3 = mCry3A, 4 = Cry3Bb1 & Cry34/35Ab1, Uk = unknown.

[3] Soil applied insecticide used, Uk = unknown.

[4] Foliar applied insecticide used, Uk = unknown.

[5] Field excluded from cropping history analyses.

Supplemental Table S3. Field history of past problem fields sampled in 2013 and 2014

	Sampled	2014	2014	2014	2014	2014	2014	2014	2014
Year	**Field #**	**1**	**2**[5]	**3**	**4**	**5**	**6**	**7**[5]	**8**
2014	**Crop**[1]	Corn	Corn	Corn	Corn	Corn	Corn	Corn	Corn
	Bt Toxin[2]	4	4	4	4	4	4	0	1
	Soil[3]	Yes	None	Yes	None	Yes	None	None	Yes
	Foliar[4]	None	None	None	None	None	None	None	None
2013	**Crop**	Corn	Corn	Corn	Corn[6]	Corn	Corn	Corn	Corn
	Bt Toxin	4	1	4	1	4	1	Uk	1
	Soil	Yes	Uk	None	None	None	None	Uk	Yes
	Foliar	None	Uk	None	None	None	None	Uk	None
2012	**Crop**	Corn	Soy	Corn	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	1	.	4	1	1	1	Uk	1
	Soil	None	.	None	None	None	None	Uk	Yes
	Foliar	None	.	None	None	None	None	Uk	None
2011	**Crop**	Corn	Corn[6]	Corn	Corn	Corn[6]	Corn[6]	Corn[6]	Corn
	Bt Toxin	1	3	4	1	1	3	1	1
	Soil	None	Uk	None	None	None	None	Uk	Yes
	Foliar	None	Uk	None	None	None	None	Uk	None
2010	**Crop**	Corn[6]	Corn	Soy	Soy	Corn	Corn	Corn	Corn
	Bt Toxin	1	1	.	.	1	1	Uk	1
	Soil	None	Uk	.	.	None	None	Uk	Yes
	Foliar	None	Uk	.	.	None	None	Uk	None
2009	**Crop**	Corn	Corn	Corn[6]	Corn	Corn	Corn	Corn	Corn[6]
	Bt Toxin	1	Uk	1	0	1	1	Uk	1
	Soil	None	Uk	None	None	None	None	Uk	None
	Foliar	None	Uk	None	None	None	None	Uk	None
2008	**Crop**	Corn	Soy	Corn	Soy	Corn	Soy	Corn	Corn
	Bt Toxin	1	.	1	.	1	.	Uk	1
	Soil	None	.	None	.	None	.	Uk	None
	Foliar	None	.	None	.	None	.	Uk	None

[1] Crop planted: Corn = Corn, Soy = Soybean; Oats = Oats; Alfa = Alfalfa; Sod = Sod, Uk = unknown.

[2] Rootworm active Bt corn: 0 = no rootworm active Bt, 1 = Cry3Bb1, 2 = Cry34/35Ab1, 3 = mCry3A, 4 = Cry3Bb1 & Cry34/35Ab1, Uk = unknown.

[3] Soil applied insecticide used, Uk = unknown.

[4] Foliar applied insecticide used, Uk = unknown.

[5] Field excluded from cropping history analyses.

[6] Year cornfield experienced greater than expected injury to Bt corn.

Supplemental Table S3 Continued. Field history of past problem fields sampled in 2013 and 2014

Year	Sampled Field #	2014 1	2014 2[5]	2014 3	2014 4	2014 5	2014 6	2014 7[5]	2014 8
2007	**Crop**[1]	Corn	Corn	Corn	Corn	Corn	Corn	Corn	Corn
	Bt Toxin[2]	1	Uk	1	0	1	Uk	Uk	1
	Soil[3]	None	Uk	None	None	None	Uk	Uk	None
	Foliar[4]	None	Uk	None	None	None	Uk	Uk	None
2006	**Crop**	Soy	Corn	Corn	Soy	Soy	Corn	Corn	Corn
	Bt Toxin	.	Uk	1	.	.	Uk	Uk	1
	Soil	.	Uk	None	.	.	Uk	Uk	None
	Foliar	.	Uk	None	.	.	Uk	Uk	None
2005	**Crop**	Corn	Corn	Corn	Corn	Corn	Soy	Corn	Corn
	Bt Toxin	1	Uk	1	0	1	.	Uk	1
	Soil	None	Uk	None	None	None	.	Uk	None
	Foliar	None	Uk	None	None	None	.	Uk	None
2004	**Crop**	Corn	Soy	Corn	Soy	Soy	Corn	Corn	Corn
	Bt Toxin	1	.	1	.	.	Uk	Uk	1
	Soil	None	.	None	.	.	Uk	Uk	None
	Foliar	None	.	None	.	.	Uk	Uk	None
2003	**Crop**	Corn	Corn	Corn	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	1	Uk	1	0	1	Uk	Uk	1
	Soil	None	Uk	None	None	None	Uk	Uk	None
	Foliar	None	Uk	None	None	None	Uk	Uk	None

[1] Crop planted: Corn = Corn, Soy = Soybean; Oats = Oats; Alfa = Alfalfa; Sod = Sod, Uk = unknown.

[2] Rootworm active Bt corn: 0 = no rootworm active Bt, 1 = Cry3Bb1, 2 = Cry34/35Ab1, 3 = mCry3A, 4 = Cry3Bb1 & Cry34/35Ab1, Uk = unknown.

[3] Soil applied insecticide used, Uk = unknown.

[4] Foliar applied insecticide used, Uk = unknown.

[5] Field excluded from cropping history analyses.

[6] Year cornfield experienced greater than expected injury to Bt corn

Supplemental Table S3 Continued. Field history of past problem fields sampled in 2013 and 2014

Year	Sampled Field #	2013 9[5]	2013 10	2013 11	2013 12	2013 13
2014	**Crop**[1]	.	.	.	.	.
	Bt Toxin[2]	.	.	.	.	.
	Soil[3]	.	.	.	.	.
	Foliar[4]	.	.	.	.	.
2013	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	4	4	4	4	4
	Soil	Uk	None	None	Yes	Yes
	Foliar	Uk	None	None	None	None
2012	**Crop**	Corn[6]	Corn[6]	Corn	Corn	Corn
	Bt Toxin	1	1	4	4	4
	Soil	Uk	None	None	None	Yes
	Foliar	Uk	Yes	None	None	Yes
2011	**Crop**	Corn	Corn	Corn[6]	Corn[6]	Corn[6]
	Bt Toxin	1	1	1	1	1
	Soil	Uk	None	None	None	Yes
	Foliar	Uk	None	None	None	Yes
2010	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	1	1	1	1	1
	Soil	Uk	None	None	None	Yes
	Foliar	Uk	None	None	None	None
2009	**Crop**	Corn	Soy	Corn	Corn	Corn
	Bt Toxin	1	.	1	1	1
	Soil	Uk	.	None	None	None
	Foliar	Uk	.	None	None	None
2008	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	1	1	1	Uk	1
	Soil	Uk	None	None	Uk	None
	Foliar	Uk	None	None	Uk	None

[1] Crop planted: Corn = Corn, Soy = Soybean; Oats = Oats; Alfa = Alfalfa; Sod = Sod, Uk = unknown.

[2] Rootworm active Bt corn: 0 = no rootworm active Bt, 1 = Cry3Bb1, 2 = Cry34/35Ab1, 3 = mCry3A, 4 = Cry3Bb1 & Cry34/35Ab1, Uk = unknown.

[3] Soil applied insecticide used, Uk = unknown.

[4] Foliar applied insecticide used, Uk = unknown.

[5] Field excluded from cropping history analyses.

[6] Year cornfield experienced greater than expected injury to Bt corn

Supplemental Table S3 Continued. Field history of past problem fields sampled in 2013 and 2014

Year	Sampled Field #	2013 9[5]	2013 10	2013 11	2013 12	2013 13
2007	**Crop**[1]	Soy	Soy	Corn	Corn	Corn
	Bt Toxin[2]	.	.	0	1	1
	Soil[3]	.	.	None	None	None
	Foliar[4]	.	.	None	None	None
2006	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	1	1	0	1	1
	Soil	Uk	None	None	None	None
	Foliar	Uk	None	None	None	None
2005	**Crop**	Soy	Soy	Corn	Soy	Corn
	Bt Toxin	.	.	0	.	1
	Soil	.	.	None	.	None
	Foliar	.	.	None	.	None
2004	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	1	Uk	0	Uk	1
	Soil	Uk	Uk	None	Uk	None
	Foliar	Uk	Uk	None	Uk	None
2003	**Crop**	Soy	Soy	Corn	Corn	Corn
	Bt Toxin	.	.	Uk	Uk	1
	Soil	.	.	Yes	Uk	None
	Foliar	.	.	None	Uk	None

[1] Crop planted: Corn = Corn, Soy = Soybean; Oats = Oats; Alfa = Alfalfa; Sod = Sod, Uk = unknown.

[2] Rootworm active Bt corn: 0 = no rootworm active Bt, 1 = Cry3Bb1, 2 = Cry34/35Ab1, 3 = mCry3A, 4 = Cry3Bb1 & Cry34/35Ab1, Uk = unknown.

[3] Soil applied insecticide used, Uk = unknown.

[4] Foliar applied insecticide used, Uk = unknown.

[5] Field excluded from cropping history analyses.

[6] Year cornfield experienced greater than expected injury to Bt corn

Supplemental Table S4. Field history of current problem fields sampled in 2013 and 2014

Year	Sampled Field #	2014 1	2014 2	2014 3	2014 4[5]
2014	**Crop**[1]	Corn	Corn	Corn	Corn
	Bt Toxin[2]	1	1	3	3
	Soil[3]	None	None	None	None
	Foliar[4]	None	None	None	None
2013	**Crop**	Corn	Corn	Corn	Corn
	Bt Toxin	1	1	1	3
	Soil	None	None	None	Uk
	Foliar	None	None	None	Uk
2012	**Crop**	Corn	Corn	Soy	Corn
	Bt Toxin	1	4	.	3
	Soil	None	None	.	Uk
	Foliar	None	None	.	Uk
2011	**Crop**	Corn	Soy	Corn	Corn
	Bt Toxin	1	.	0	Uk
	Soil	None	.	None	Uk
	Foliar	None	.	None	Uk
2010	**Crop**	Soy	Corn	Sod	Corn
	Bt Toxin	.	1	.	Uk
	Soil	.	None	.	Uk
	Foliar	.	None	.	Uk
2009	**Crop**	Corn	Corn	Sod	Corn
	Bt Toxin	1	Uk	.	Uk
	Soil	None	None	.	Uk
	Foliar	None	None	.	Uk
2008	**Crop**	Corn	Corn	Sod	Corn
	Bt Toxin	1	Uk	.	Uk
	Soil	None	None	.	Uk
	Foliar	None	None	.	Uk

[1] Crop planted: Corn = Corn, Soy = Soybean; Oats = Oats; Alfa = Alfalfa; Sod = Sod, Uk = unknown.

[2] Rootworm active Bt corn: 0 = no rootworm active Bt, 1 = Cry3Bb1, 2 = Cry34/35Ab1, 3 = mCry3A, 4 = Cry3Bb1 & Cry34/35Ab1, Uk = unknown.

[3] Soil applied insecticide used, Uk = unknown.

[4] Foliar applied insecticide used, Uk = unknown.

[5] Field excluded from cropping history analyses.

Supplemental Table S4 Continued. Field history of current problem fields sampled in 2013 and 2014

Year	Sampled Field #	2014 1	2014 2	2014 3	2014 4[5]
2007	**Crop**[1]	Corn	Corn	Sod	Corn
	Bt Toxin[2]	1	Uk	.	Uk
	Soil[3]	None	None	.	Uk
	Foliar[4]	None	None	.	Uk
2006	**Crop**	Corn	Soy	Sod	Corn
	Bt Toxin	1	.	.	Uk
	Soil	None	.	.	Uk
	Foliar	None	.	.	Uk
2005	**Crop**	Soy	Corn	Sod	Corn
	Bt Toxin	.	0	.	Uk
	Soil	.	None	.	Uk
	Foliar	.	None	.	Uk
2004	**Crop**	Corn	Alfa	Corn	Corn
	Bt Toxin	1	.	0	Uk
	Soil	None	.	None	Uk
	Foliar	None	.	None	Uk
2003	**Crop**	Corn	Alfa	Corn	Corn
	Bt Toxin	1	.	0	Uk
	Soil	None	.	None	Uk
	Foliar	None	.	None	Uk

[1] Crop planted: Corn = Corn, Soy = Soybean; Oats = Oats; Alfa = Alfalfa; Sod = Sod, Uk = unknown.

[2] Rootworm active Bt corn: 0 = no rootworm active Bt, 1 = Cry3Bb1, 2 = Cry34/35Ab1, 3 = mCry3A, 4 = Cry3Bb1 & Cry34/35Ab1, Uk = unknown.

[3] Soil applied insecticide used, Uk = unknown.

[4] Foliar applied insecticide used, Uk = unknown.

[5] Field excluded from cropping history analyses.

Supplemental Table S4 Continued. Field history of current problem fields sampled in 2013 and 2014

Year	Sampled Field #	2013 5[5]	2013 6	2013 7	2013 8	2013 9
2014	**Crop**[1]	.	.	.	.	.
	Bt Toxin[2]	.	.	.	.	.
	Soil[3]	.	.	.	.	.
	Foliar[4]	.	.	.	.	.
2013	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	1	1	1	1	1
	Soil	None	None	None	None	None
	Foliar	None	None	None	None	None
2012	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	1	1	4	1	1
	Soil	None	None	None	None	None
	Foliar	None	None	None	None	None
2011	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	1	1	1	0	1
	Soil	None	None	None	None	None
	Foliar	None	None	None	None	None
2010	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	Uk	0	1	0	1
	Soil	Uk	None	None	None	None
	Foliar	Uk	None	None	None	None
2009	**Crop**	Soy	Soy	Corn	Corn	Corn
	Bt Toxin	.	.	1	0	1
	Soil	.	.	None	None	None
	Foliar	.	.	None	None	None
2008	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	Uk	0	1	0	1
	Soil	Uk	None	None	None	None
	Foliar	Uk	None	None	None	None

[1] Crop planted: Corn = Corn, Soy = Soybean; Oats = Oats; Alfa = Alfalfa; Sod = Sod, Uk = unknown.

[2] Rootworm active Bt corn: 0 = no rootworm active Bt, 1 = Cry3Bb1, 2 = Cry34/35Ab1, 3 = mCry3A, 4 = Cry3Bb1 & Cry34/35Ab1, Uk = unknown.

[3] Soil applied insecticide used, Uk = unknown.

[4] Foliar applied insecticide used, Uk = unknown.

[5] Field excluded from cropping history analyses.

Supplemental Table S4 Continued. Field history of current problem fields sampled in 2013 and 2014

Year	Sampled Field #	2013 5[5]	2013 6	2013 7	2013 8	2013 9
2007	**Crop**[1]	Soy	Soy	Corn	Corn	Corn
	Bt Toxin[2]	.	.	1	Uk	1
	Soil[3]	.	.	None	Uk	None
	Foliar[4]	.	.	None	Uk	None
2006	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	Uk	0	1	Uk	1
	Soil	Uk	None	None	Uk	None
	Foliar	Uk	None	None	Uk	None
2005	**Crop**	Soy	Soy	Corn	Soy	Corn
	Bt Toxin	.	.	0	.	1
	Soil	.	.	None	.	None
	Foliar	.	.	None	.	None
2004	**Crop**	Corn	Corn	Corn	Corn	Corn
	Bt Toxin	Uk	0	0	Uk	1
	Soil	Uk	None	None	Uk	None
	Foliar	Uk	None	None	Uk	None
2003	**Crop**	Soy	Soy	Corn	Soy	Corn
	Bt Toxin	.	.	0	.	1
	Soil	.	.	None	.	None
	Foliar	.	.	None	.	None

[1] Crop planted: Corn = Corn, Soy = Soybean; Oats = Oats; Alfa = Alfalfa; Sod = Sod, Uk = unknown.

[2] Rootworm active Bt corn: 0 = no rootworm active Bt, 1 = Cry3Bb1, 2 = Cry34/35Ab1, 3 = mCry3A, 4 = Cry3Bb1 & Cry34/35Ab1, Uk = unknown.

[3] Soil applied insecticide used, Uk = unknown.

[4] Foliar applied insecticide used, Uk = unknown.

[5] Field excluded from cropping history analyses.

CHAPTER 5.

INCREASED RISK OF INSECT INJURY TO CORN FOLLOWING RYE COVER CROP

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Abstract

Decreased pest pressure is sometimes associated with more diverse agroecosystems, including the addition of a rye cover crop (*Secale cereale* L.). However, not all pests respond similarly to greater vegetational diversity. Polyphagous pests, such as true armyworm (*Mythimna unipuncta*), black cutworm (*Agrotis ipsilon*) and common stalk borer (*Papaipema nebris*), whose host range includes rye, have the potential to cause injury to crops following a rye cover crop. The objectives of this study were to compare the abundance of early season insect pests and injury to corn (*Zea mays* L.) from fields with and without a rye cover crop on commercial farms. Fields were sampled weekly to quantify adult and larval pests and defoliation to corn plants from mid-April until corn reached V8 stage, during 2014 and 2015. Measurements within fields were collected along transects that extended perpendicularly from field edges into the interior of cornfields. Adult true armyworm and adult black cutworm were captured around all cornfields, but most lepidopteran larvae captured within cornfields were true armyworm and common stalk borer. Cornfields with a rye cover crop had significantly greater abundance of true armyworm and greater proportion of defoliated corn. Both true armyworm abundance and feeding injury were significantly greater in the interior of cornfields with rye. Common stalk borer abundance did not differ between

cornfields with or without rye cover. Farmers planting corn following a rye cover crop should be aware of the potential for increased presence of true armyworm and for greater injury to corn.

Introduction

Decreased pest abundance is associated with more diverse agroecosystems (Root 1973, Andow 1991a, Landis et al. 2000). Diversity in agroecosystems can be measured by the number of species present, the spatial arrangement of species, the temporal relationship among species, or combinations of these factors (Andow 1991a). The scale at which cropping diversity is measured also can vary from the landscape level, to fields, or to individual plants. Greater landscape heterogeneity can increase habitat quality for natural enemies, especially when the area planted to annual monoculture decreases (Landis et al. 2000). Furthermore, increasing the connectivity of suitable habitat within landscapes may enable natural enemies to move and colonize new areas (Frampton et al. 1995). For example, parasitism rates were significantly higher for *Mythimna unipuncta* Haworth (Lepidoptera: Noctuidae), true armyworm, larvae released and recaptured from complex landscapes containing small agricultural fields, hedgerows, and woodlots compared to larvae released and recaptured in simple landscapes dominated by agricultural fields (Marion and Landis 1996). The addition of a second crop or non-crop species increases diversity within fields, and farming practices that promote intra-field diversity include intercropping, weedy culture, and the addition of cover crops (Andow 1991b). Recent literature reviews suggest that greater vegetational diversity within fields generally has a positive effect on natural enemy abundance and a negative effect on the abundance of insect pests (Sunderland and Samu 2000, Symondson et al. 2002, Langellotto and Denno 2004, Letourneau et al. 2011).

The addition of cover crops to agroecosystems can reduce soil erosion and water runoff from fields (Kasper et al. 2001, Hartwig and Ammon 2002) and limit nitrate leaching (Owens et al. 2000). Furthermore, planting a cover crop also increases vegetational diversity within fields (Andow 1991b). Cover crops can positively affect predator abundance within fields (Prasifka et al. 2006, Schmidt et al. 2007) and negatively affect the abundance of insect pests (Tillman et al. 2004, Koch et al. 2012). Rye (*Secale cereale* L.) is planted as a cover crop in the U.S. Corn Belt because of its cold hardiness and early regrowth during the spring (Bollero and Bullock 1994, Dinnes et al. 2002). In the Corn Belt, a rye cover crop is most commonly planted during the fall and terminated in spring before the cash crop is planted (Clark 2007, USDA, NRCS 2013a).

A rye cover crop can reduce insect pest pressure, though the mechanisms for this are not always discernible. The enemies hypothesis predicts that pests should be less abundant in polycultures because natural enemies are more abundant in polycultures compared to monocultures (Root 1973). However, there are observations in which the addition of a rye cover crop resulted in lower pest abundance without a concurrent significant increase in natural enemy abundance (Bottenberg et al. 1997, Koch et al. 2012). Not all pests respond similarly to agroecosystem diversification, and host range is one factor that can alter a pest's response to polyculture. The abundance of monophagous pests is predicted to be lower in more diverse cropping systems compared to monocultures (Root 1973, Risch et al. 1983, Andow 1991). The resource concentration hypothesis predicts that monophagous pests would be more successful in monocultures than in a more diverse agroecosystem based on their capacity to find their host plant (Root 1973). The response of polyphagous pests to greater

vegetational diversity in agroecosystems is complex (Andow 1991a) and varies widely among pest species (Risch 1980, Andow 1990, 1991a).

Polyphagous pests associated with rye have the potential to injure a cash crop when rye is added as a cover crop. There are several species of noctuid moths with host ranges that include rye: true armyworm, *Agrotis ipsilon* Hufnagel (Lepidoptera: Noctuidae), black cutworm, and *Papaipema nebris* Guenee (Lepidoptera: Noctuidae), common stalk borer. In addition to their ability to feed on rye, all are early season pests of corn (Willson and Eisley 1992, Showers 1997, Rice and Davis 2010). Black cutworm and common stalk borer are highly polyphagous and can complete development on hosts from several plant families (Highland and Roberts 1987, Showers 1997, Rice and Davis 2010). True armyworm is associated primarily with grasses (Poaceae), though its host range also includes other families (Capinera 2008). True armyworm and black cutworm do not overwinter in the Corn Belt, and both migrate northward from southern states each year during early spring (Hendrix III and Showers 1992). Oviposition by true armyworm and black cutworm occurs on grasses and weeds before corn is planted (Showers 1997, Capinera 2008), and black cutworm also will lay eggs on plant debris (Showers 1997). Common stalk borer successfully overwinter in the Corn Belt, diapausing as eggs that have been oviposited on dead vegetation during the fall (Levine 1985, Rice and Davis 2010). Larvae of each species can defoliate young, vegetative corn. Additionally, black cutworm and common stalk borer larvae injury corn by cutting stalks and tunneling into plants.

Each of these pests is affected by agronomic practices that alter host-plant diversity within fields, such as the destruction of weed populations, tillage, and planting of cover crops (Rice and Pedigo 1997, Showers 1997, Capinera 2008). Cultural practices that allow for

weeds to exist within fields can increase the risk of injury to corn from black cutworm and common stalk borer (Shower 1997, Rice and Davis 2010) as removal of weeds may force black cutworm and common stalk borer larvae migration to corn plants (Showers et al. 1985, Rice and Davis 2010). True armyworm injury to corn is more frequent in fields without tillage that were previously planted to a grassy crop (Harrison et al. 1980, Willson and Eisley 1992). The current recommendations for the use of rye as a cover crop (MCCC 2012, USDA, NRCS 2013a) are intended to prevent the likelihood of overlap between rye and corn, which could reduce corn yield due to competition (Tollenaar et al. 1993). Whether this recommendation will decrease the risk of injury to corn from these pests is not clear, especially given the challenges that farmers can face in timely removal of a cover crop and planting of the primary crop. In this study, we conducted on-farm research to compare the abundance of early-season insect pests and injury to corn between cornfields with and without a rye cover crop. We hypothesized that the addition of a rye cover crop to cornfields would increase the abundance of lepidopteran pest species. Furthermore, we hypothesized that injury to corn in fields including a rye cover crop would be greater compared to cornfields without a cover crop.

Materials and Methods

Data Collection. Cornfields were sampled for early season insect pests and injury to corn on commercial farms in Iowa during 2014 and 2015. Cooperators were identified by members of the agricultural community including Iowa State University extension personnel, Practical Farmers of Iowa, and local cooperators. All cornfields sampled were planted to non-Bt corn hybrids. Corn was either planted following a rye cover crop or into a field without a cover crop. The timing and method of termination for the rye is reported in Table

1. Although fields did not receive insecticide applications in 2014, insecticide was applied to foliage in three of the six cornfields with a rye cover crop in 2015 to manage true armyworm populations. In each of these three cornfields, insecticides were applied once between 18 May and 1 June. For these fields, data on larval abundance recorded after application of insecticide were excluded from all analyses.

Cornfields were sampled weekly each year beginning in mid-April until corn reached the V8 developmental stage (Abendroth et al. 2011), which occurred in late June and early July. This stage was selected because corn exceeding the V6 to V8 stage is considered large enough to tolerate injury from true armyworm, black cutworm, and common stalk borer (Showers et al. 1983, Mulder and Showers 1986, Davis and Pedigo 1991).

Data were collected on farming practices within fields, including tillage, application of pesticides, planting date of corn, and emergence of corn plants. Data also were collected weekly on percentage of ground cover, presence of adult and larval pests, insect injury to corn plants, status of the rye cover crop (live or dead) and corn developmental stage. These weekly measurements were taken along a single transect that ran from the edge of each field to the interior. Transects began at a arbitrarily selected location at the boarder of each field and extended perpendicularly 80 m into the interior of a field with samples taken every 20 m (0 m [field edge], 20 m, 40 m, 60 m, and 80 m). At each sampling interval, a quadrat (i.e., pvc pipe frame (0.6 m × 1.5 m) was placed on the ground and data collected on the area inside the quadrat (Laub and Luna 1991). When corn emerged within fields, the quadrat was centered over a single row of corn and contained 5.4 ± 0.1 corn plants (mean ± SEM; N = 779 samples).

Measurements of percent ground cover included total ground cover and rye ground cover. Total ground cover included everything that covered the soil surface, including plant debris, weeds, corn, and rye. Rye ground cover was defined as the percentage of the ground covered by the rye cover crop, and including both live and dead rye plants. Both total ground cover and rye ground cover were visually estimated to the nearest five percent. The soil surface and all plant material within quadrats were searched for lepidopteran larvae. All larvae were captured, stored in 85% ethanol and identified to species. Data were collected on feeding injury to each corn plant within a quadrat, including the number of plants that displayed feeding injury, and the percentage of leaf area consumed on each plant. The percentage of leaf area consumed was estimated to the nearest five percent based on visual inspection.

Species-specific sex pheromone wing traps (Trece Inc., Adiar, OK) were used to sample true armyworm and black cutworm adults to estimate the potential for true armyworm and black cutworm larvae to be found within cornfields. Two wing traps per species were placed around the border of each cornfield. Traps were changed weekly and pheromone lures within traps were changed every fourth week.

Data Analysis. All analyses were performed in SAS statistical software version 9.3 (SAS Institute, Cary, North Caroline). Total ground cover within cornfields, adult true armyworm abundance, and adult black cutworm abundance were each analyzed separately by year with repeated measures analysis of variance (ANOVA) (PROC MIXED). Fixed effects in the model were cover treatment (rye cover crop vs. no cover crop), sampling week, and their interaction. Sampling week was used as a repeated measure with compound symmetry covariance structure. Random factors in the analysis included location nested within cover

treatment and the interaction of sampling week and location nested in cover treatment. Data were transformed by the Log (x + 0.5) function to ensure normality of the residuals. When significant effects were present, pairwise comparisons were made using the PDIFF option in PROC MIXED. Alpha levels were adjusted for multiple comparisons using the Bonferroni correction. For cornfields with a rye cover crop, the percentage of rye ground cover within fields was analyzed with repeated measures ANOVA (PROC MIXED). Model effects were identical to the analysis of total ground cover, but excluded the effect of cover treatment. Data on percent rye ground cover were also transformed by the Log (x + 0.5) function to ensure normality of the residuals. The LSMEANS statement was used to test if rye cover during each sampling week was significantly different from zero.

Variances for larval abundance and feeding injury to corn were heterogeneous even after data were transformed, therefore analyses were performed with nonparametric Mann-Whitney-Wilcoxon test (PROC NPAR1WAY). Mann-Whitney-Wilcoxon tests were used to compare the effect of cover treatment on the overall abundance of larvae, larval abundance by sampling week, and larval abundance by distance measured along transects. Data were analyzed separately for each species. Furthermore, analyses also were conducted to test the effect of cover treatment on the percentage of corn plants that displayed feeding injury and the percentage of leaf area consumed on each defoliated plant. Data from 2014 and 2015 were analyzed separately for larval abundance by sampling week, but years were combined for all other analyses. To conserve statistical power, tests of larval abundance by sampling week were only performed for weeks when both corn and larvae were present within fields. Alpha levels were adjusted for multiple comparisons using the Bonferroni correction based on the number of comparisons.

Results

Ground Cover. In both 2014 and 2015, total ground cover did not significantly differ between cornfields that had a rye cover crop and those that did not (Table 2; Figs. 1A and 1B). In 2014, the percentage of rye ground cover in fields with a rye cover crop changed significantly over time ($F = 17.5$; df = 10, 90; $P < 0.0001$). The majority of rye cover crops within fields were terminated by the fourth week of sampling (12 May; Table 1) and after the fourth week of sampling, the percentage of rye ground cover did not differ significantly from zero (Fig. 1A). In 2015, rye ground cover within fields also differed significantly over time ($F = 3.98$; df = 8, 36; $P = 0.0019$). The rye cover crops were terminated earlier than in 2014 (Table 1), though rye ground cover was significantly greater than zero within cornfields two weeks after termination and during the final week of sampling (Fig. 1B).

Lepidopteran Community. During both 2014 and 2015, adult true armyworm and black cutworm were captured at all cornfields sampled regardless of the presence or absence of a rye cover crop. Pheromone traps set in 2014 captured true armyworm (Fig. 2A) and black cutworm (Fig. 2B) migrating into Iowa throughout April and early May. There was no significant difference in the abundance of adult true armyworm or black cutworm captured between cornfields with or without a rye cover crop in 2014 (Table 3). By contrast, in 2015 the number of true armyworm (Fig. 2A) and black cutworm (Fig. 2B) captured was significantly greater for cornfields with a rye cover crop.

Larvae of six lepidopteran species were collected in cornfields. The majority of larvae captured during the study, 82%, were captured from fields that had a rye cover crop (Table 4). In 2014, the majority of larvae captured were true armyworm (42%) and common stalk borer (42%), while only one black cutworm larvae was found (Table 4). Three other species

were collected in 2014; *Hyena scabra* Fabricius (Lepidoptera: Erebidae), green cloverworm, *Feltia jaculifera* Guenee (Lepidoptera: Noctuidae), dingy cutworm, and *Spodoptera frugiperda* Smith (Lepidoptera: Noctuidae), fall armyworm (Table 4). Three species of larvae were collected from cornfields in 2015, of which true armyworm represented 80% of larvae captured (Table 4). Common stalk borer represented 19% of larvae captured. Again, there was only a single black cutworm larva collected.

Larval Distribution within Fields. True armyworm larvae were significantly more abundant in cornfields that had a rye cover crop ($Z = 4.28$; $P < 0.0001$). Ninety-six of the 102 true armyworm larvae were collected from fields that had a rye cover crop (Table 4). Furthermore, there were significantly more true armyworm larvae captured in the interior of cornfields with a rye cover crop than cornfields without a cover crop (Fig. 3A). True armyworm larvae were significantly more abundant at 60 m ($Z = 2.61$; $P = 0.028$) and 80 m ($Z = 2.60$; $P = 0.028$) into the interior of fields that had a rye cover crop. In cornfields without a rye cover crop, true armyworm was captured only at field edges. Difference in true armyworm abundance were significant only once when compared between field types over time, with significantly more larvae found in fields with a rye cover crop during the ninth week of sampling in 2014 (Table 5).

Common stalk borer larval abundance did not differ between cornfields with or without a rye cover crop ($Z = 0.01$; $P = 0.99$). These larvae were almost exclusively found at the edges of cornfields, and abundance of larvae did not differ between fields with and without rye cover at any distance along transects (Fig. 3B). Additionally, there were no differences in abundance of common stalk borer larvae between field types over time (Table

5). Black cutworm larvae were rare (Table 4), therefore no statistical analyses were performed for black cutworm larvae.

Corn Defoliation. There was a significantly greater proportion of defoliated corn plants in fields that had a rye cover crop ($Z = 5.89$; $P < 0.0001$). Proportion of defoliated corn plants was also significantly greater in fields with a rye cover crop when sampled at 40 m ($Z = 3.11$; $P = 0.011$), 60 m ($Z = 3.97$; $P < 0.0001$), and 80 m ($Z = 3.35$; $P = 0.005$) from field edges (Fig. 4). For corn plants that were defoliated by insect larvae, the percentage of leaf area consumed did not differ between fields with and without a rye cover crop ($Z = 0.02$; $P = 0.92$).

Discussion

From two years of sampling commercial cornfields, we observed a significant increase in the occurrence of an early season lepidopteran pest and defoliation of corn in cornfields that followed a rye cover crop. These results support the hypothesis that rye as a cover crop in cornfields increases the abundance of an early season pest. However, true armyworm was the only early season pest to respond significantly to the presence of a rye cover crop within fields (Fig. 3A). Common stalk borer abundance was not affected by the presence of the rye cover crop (Fig. 3B) and other lepidopteran larvae were rare (Table 4). These data also support the hypotheses that the use of rye as a cover crop in cornfields would increase the incidence of injury to corn, as there were significantly more defoliated corn plants present in fields that included a rye cover crop (Fig. 4).

There was no significant difference in common stalk borer abundance between cornfields with or without a rye cover crop (Fig. 3B). Female common stalk borer preferentially oviposit on thin-stemmed, perennial grasses compared to annual, wide-leaved

grasses (such as rye) or broad-leaved plants (Levine 1985, Highland and Roberts 1989, Rice and Davis 2010). The majority of common stalk borer eggs are deposited throughout the fall between curled leaves and stems, most frequently on dead vegetation (Levine 1985). Common stalk borer oviposition appears unlikely to occur within fields with a rye cover crop given that common stalk borer larvae were rarely observed in the interior of cornfields (Fig. 3B). Injury to corn by common stalk borer is typically limited to field margins where corn is found adjacent to grass waterways, ditches, or terraces (Davis and Pedigo 1990, Meyer and Peterson 1998). Destruction of weedy host plants by herbicides can facilitate common stalk borer movement into cornfields (Levine 1993) and studies have shown common stalk borer larvae readily consume and tunnel into rye plants (Highland and Roberts 1987). However, the abundance of common stalk borer larvae at field edges (Fig. 3B) and the incidence of defoliated corn plants at field edges (Fig. 4) both did not differ between cornfields with or without a rye cover crop. Therefore, the use of a rye cover crop did not facilitate injury to corn by common stalk borer.

True armyworm larvae were found in significantly greater abundance in the interior of cornfields planted with a rye cover crop (Fig. 3A). In cornfields without a rye cover crop, true armyworm larvae were most frequently captured at field edges (Fig. 3A) even though larvae are highly mobile (Capinera 2008). Defoliation of corn plants was significantly greater throughout cornfields that contained a rye cover crop (Fig. 4). As common stalk borer was predominately found at field edges (Fig. 3B) and the presence of other lepidopteran larvae was rare (Table 4), defoliation injury to corn in the interior of fields can be attributed primarily to true armyworm (Figs. 3A and 4).

When corn is planted following a rye cover crop, timing of rye termination is considered critical to preventing negative impacts on corn development (Raimbault et al. 1990, Tollenaar et al. 1993, MCCC 2012). Early termination of a rye cover crop is thought to reduce the risk of injury to corn by true armyworm because eggs oviposited prior to the rye's termination hatch without sufficient food and may starve before corn emerges (MCCC 2012). However, our data indicate that early termination of a rye cover crop did not ameliorate the risk of true armyworm injury to corn (Table 1; Fig. 3A).

There are limited preventative management tactics available to farmers for true armyworm and some of the other lepidopteran larvae that we observed. At present there are no seed treatments labeled for either true armyworm or common stalk borer management, though most seed treatments offer at least some suppression of black cutworm (Smith and Proost 2011). Furthermore, there are no genetically modified corn hybrids expressing *Bacillus thuringiensis* (Bt) toxins that are labeled for true armyworm management (Cullen et al. 2013). Greenhouse and field trials have demonstrated that Bt corn hybrids expressing Cry1Ab (events Mon810 and Bt176) and Cry1F (event TC1507) each experienced less true armyworm injury compared to their respective non-Bt isolines (Schaafsma et al. 2007). There are corn hybrids expressing Bt toxins that are labeled for management of common stalk borer and black cutworm (Cullen et al. 2013). Field trials have shown that insecticides including organophosphate (chlorpyrifos and acephate) applied at planting can provide protection from true armyworm injury to corn following a rye cover crop (Harrison et al. 1980).

Since true armyworm sporadically reach high densities, in irregular intervals anywhere between 5 and 20 years apart (Guppy 1961, Capinera 2008), the prophylactic use of insecticides is likely not cost effective. An alternative approach could include integrative

pest management strategies, such as scouting for true armyworm larvae and injury, economic thresholds for treatment decisions (Varenhorst et al. 2015), and farm management practices that conserve beneficial arthropods (Marion and Landis 1996, Landis et al. 2000). The farmers who experienced higher true armyworm larval abundance and corn defoliation in 2015 used a foliar-applied, pyrethroid insecticide (lambda-cyhalothrin or zeta-cypermethrin), and true armyworm populations were suppressed successfully in each case (M. Dunbar, *personal observation*).

Rye is beneficial as a cover crop because it is cold hardy, begins rapid regrowth early in the spring, and readily scavenges excess soil nitrates (Bollero and Bullock 1994, Strock et al. 2004, Clark 2007). Landscape-level adoption of cover crops has been predicted to substantially reduce movement of nitrogen from croplands into the water table, thereby reducing negative downstream effects of excess nitrogen (USDA, NRCS 2013b). Despite these benefits, adoption of rye as a cover crop throughout the Corn Belt is limited. Low adoption of rye may be explained in part by the cost of establishment/ termination and the risk of competition between rye and a cash crop (Tollenaar et al. 1993, De Bruin et al. 2005). Farmers that grow cover crops can receive financial aid to offset the initial costs of establishing a cover crop through the Environmental Quality and Incentives Plan (EQIP) (USDA, NRCS 2015). Furthermore, farmers can attach insurance to cash crops that follows a cover crop under certain conditions (USDA, RMA 2014), such as the timing of cover crop termination based on geographic zones (USDA, NRCS 2013c). These termination guidelines are purposefully broad as to encompass the numerous combinations of cash crop and cover crop. However, farmers planting corn following a rye cover crop should be aware of the potential effect of rye cover crop on injury to corn from true armyworm.

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Tables

Table 1. Number of cornfields sampled and crop phenology during 2014 and 2015

		2014	2015
Cornfields sampled		16	11
Rye cover crop		10	6
Termination method	Herbicide	5	5
	Tillage	5	1
No cover crop		6	5
# Weeks sampled		11	9
Start Week		14 April	13 April
End Week		30 June	15 June
50% Rye termination [a]		12 May	20 April
50% Corn emergence			
Rye cover crop fields		26 May	11 May
No cover crop fields		19 May	11 May

[a] The date at which the rye cover crop is terminated in > 50% of the fields sampled

Table 2. Analysis of variance for total ground cover during 2014 and 2015

Year	Effect	*F*	df	*P*
2014				
	Cover Treatment	2.09	1, 14	0.17
	Sampling Week	4.91	10, 140	**<0.0001**
	Cover*Week	0.57	10, 140	0.84
2015				
	Cover Treatment	0.80	1, 9	0.40
	Sampling Week	4.08	8, 64	**0.0006**
	Cover*Week	1.52	8, 64	0.17

Table 3. Analysis of variance for adult true armyworm (TAW) and black cutworm (BCW) during 2014 and 2015

Year	Species	Effect	*F*	df	*P*
2014	TAW				
		Cover Treatment	0.01	1, 14	0.92
		Sampling Week	12.13	10, 138	**<0.0001**
		Cover*Week	0.73	10, 138	0.70
	BCW				
		Cover Treatment	0.86	1, 14	0.37
		Sampling Week	14.32	10, 138	**<0.0001**
		Cover*Week	0.53	10, 138	0.87
2015	TAW				
		Cover Treatment	5.88	1, 8	**0.042**
		Sampling Week	29.51	8, 56	**<0.0001**
		Cover*Week	1.54	8, 56	0.16
	BCW				
		Cover Treatment	8.86	1, 8	**0.018**
		Sampling Week	25.20	8, 56	**<0.0001**
		Cover*Week	0.96	8, 56	0.48

Table 4. Larvae captured by year from cornfields with and without a rye cover crop

Year	Family	Species		No Cover	Rye Cover
2014					
	Erebidae	*Hypena scabra*	Green cloverworm	0	1
	Noctuidae	*Agrotis ipsilon*	Black cutworm	0	1
		Feltia jaculifera	Dingy cutworm	0	1
		Mythimna unipuncta	True armyworm	1	19
		Papaipema nebris	Common stalk borer	6	14
		Spodoptera frigiperda	Fall armyworm	0	4
2015					
	Noctuidae	*Agrotis ipsilon*	Black cutworm	1	0
		Mythimna unipuncta	True armyworm	5	77
		Papaipema nebris	Common stalk borer	13	6

Table 5. Mean larval abundance (± standard error of the mean) by sampling week from cornfields with and without a rye cover crop during 2014 and 2015

Week	True armyworm			Common stalk borer		
Sampled	No Cover	Rye Cover		No Cover	Rye Cover	
2014						
(June)[a] Wk 7	0.0 (±0.0)	0.0 (±0.0)	.	0.0 (±0.0)	0.0 (±0.0)	.
Wk 8	0.0 (±0.0)	0.02 (±0.1)	$Z = 0.8$; $P = 1.0$[b]	0.0 (±0.0)	0.0 (±0.0)	.
Wk 9	0.03 (±0.1)	0.3 (±0.1)	$Z = 2.8$; $P = 0.04$	0.0 (±0.0)	0.02 (±0.1)	$Z = 0.8$; $P = 1.0$
Wk 10	0.0 (±0.0)	0.04 (±0.1)	$Z = 1.1$; $P = 1.0$	0.0 (±0.0)	0.08 (±0.1)	$Z = 1.1$; $P = 1.0$
(July) Wk 11	0.0 (±0.0)	0.0 (±0.0)	.	0.07 (±0.1)	0.10 (±0.1)	$Z = 0.5$; $P = 1.0$
Wk 12	0.0 (±0.0)	0.02 (±0.1)	$Z = 0.8$; $P = 1.0$	0.13 (±0.1)	0.08 (±0.1)	$Z = 0.5$; $P = 1.0$
2015						
(May) Wk 4	0.0 (±0.0)	0.0 (±0.0)	.	0.0 (±0.0)	0.0 (±0.0)	.
Wk 5	0.0 (±0.0)	0.0 (±0.0)	.	0.0 (±0.0)	0.0 (±0.0)	.
Wk 6	0.0 (±0.0)	0.6 (±0.2)	$Z = 2.3$; $P = 0.08$	0.08 (±0.1)	0.07 (±0.1)	$Z = 0.1$; $P = 1.0$
(June) Wk 7	0.04 (±0.1)	0.4 (±0.2)	$Z = 1.7$; $P = 0.3$	0.08 (±0.1)	0.04 (±0.1)	$Z = 0.01$; $P = 1.0$
Wk 8	0.02 (±0.1)	3.3 (±1.2)	$Z = 2.2$; $P = 0.12$	0.0 (±0.0)	0.13 (±0.1)	$Z = 0.7$; $P = 1.0$
Wk 9	0.01 (±0.1)	0.01 (±0.1)	$Z = 0.4$; $P = 1.0$	0.20 (±0.1)	0.10 (±0.1)	$Z = 0.04$; $P = 1.0$
Wk 10	0.0 (±0.0)	0.0 (±0.0)	.	0.20 (±0.1)	0.0 (±0.0)	$Z = 1.1$; $P = 1.0$

[a] Denotes the month in which sampling weeks occurred.

[b] Mann-Whitney-Wilcoxon test results comparing differences between larval abundance from cornfields with and without a rye cover crop. Tests were only performed during sampling weeks when both corn and larvae were present within fields.

Figures

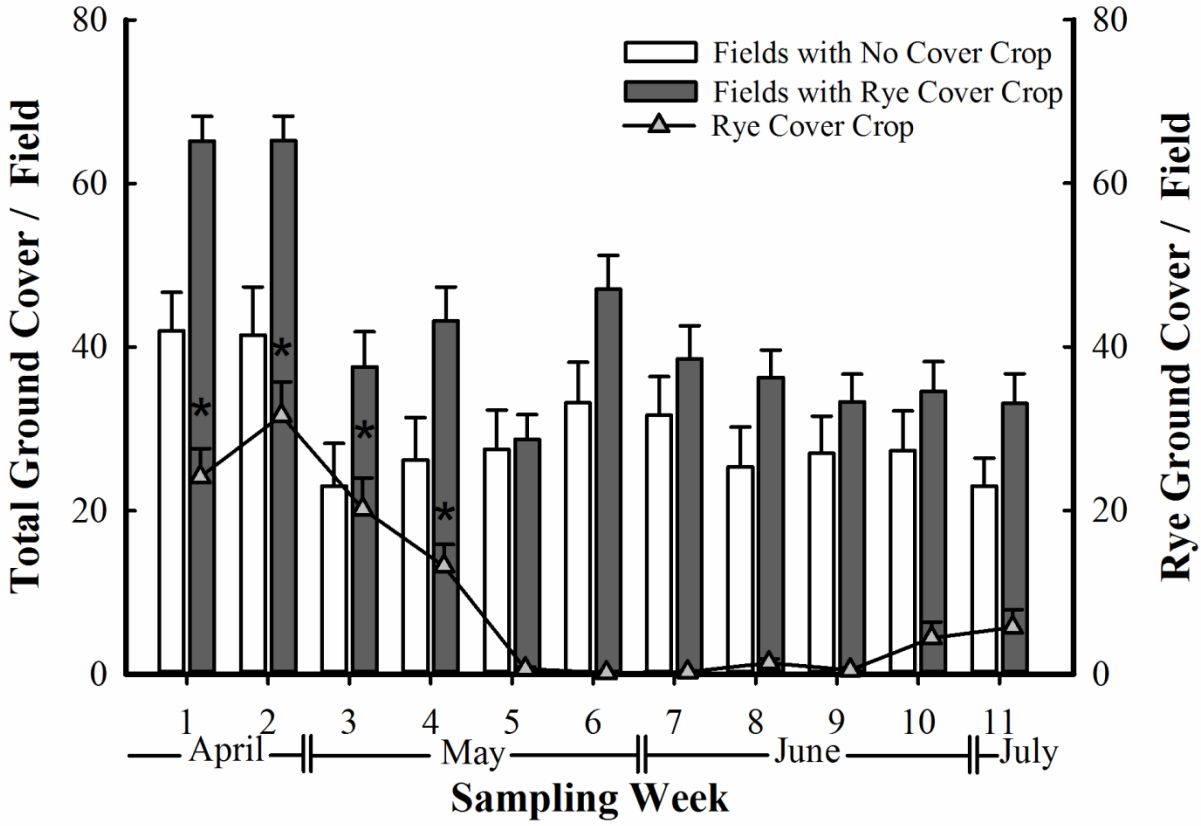

Figure 1A. Total ground cover and rye ground cover in cornfields from 2014 (A) and 2015 (B). Bar heights and points represent sample means and error bars are the standard error of the means. Stars represent sampling weeks when the percentage of rye ground cover was significantly greater than 0%.

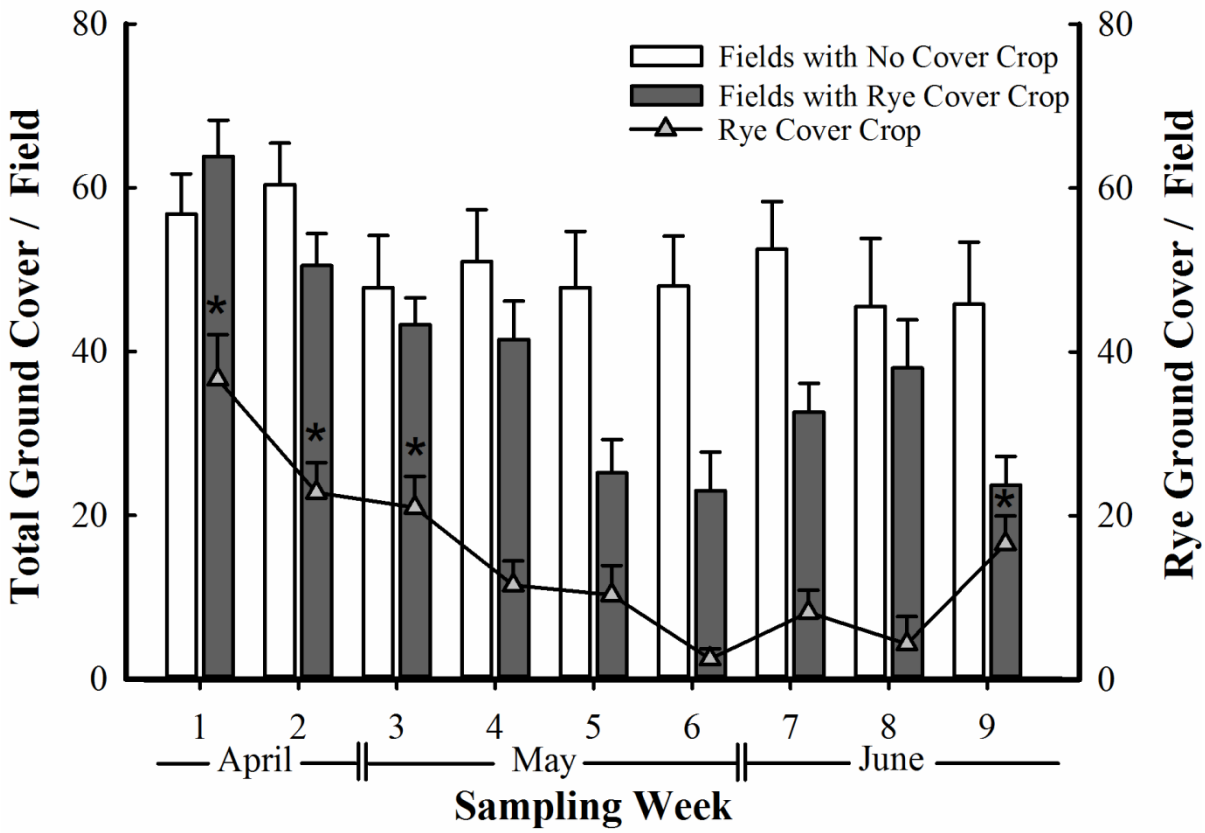

Figure 1B. Total ground cover and rye ground cover in cornfields from 2014 (A) and 2015 (B). Bar heights and points represent sample means and error bars are the standard error of the means. Stars represent sampling weeks when the percentage of rye ground cover was significantly greater than 0%.

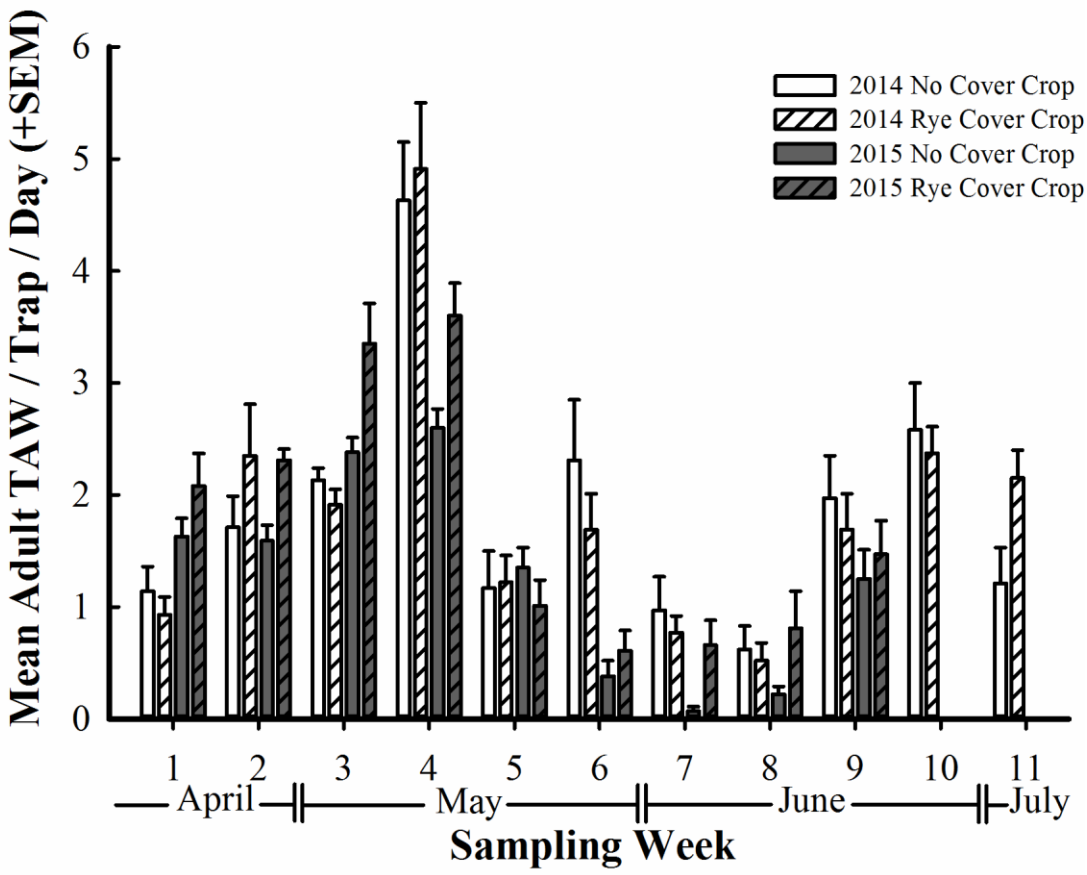

Figure 2A. Adult true armyworm (TAW) (A) and black cutworm (BCW) (B) captured by pheromone traps during 2014 and 2015. Bar heights represent sample means and error bars are the standard error of the means.

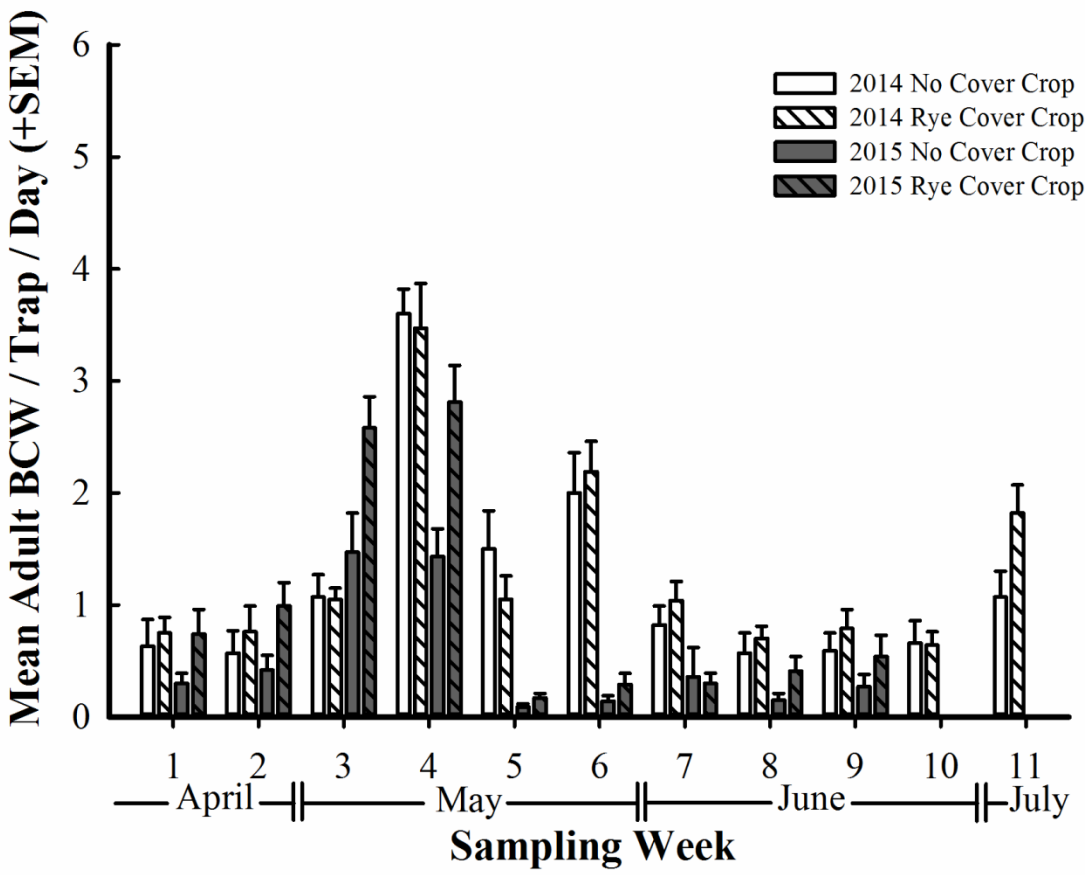

Figure 2B. Adult true armyworm (TAW) (A) and black cutworm (BCW) (B) captured by pheromone traps during 2014 and 2015. Bar heights represent sample means and error bars are the standard error of the means.

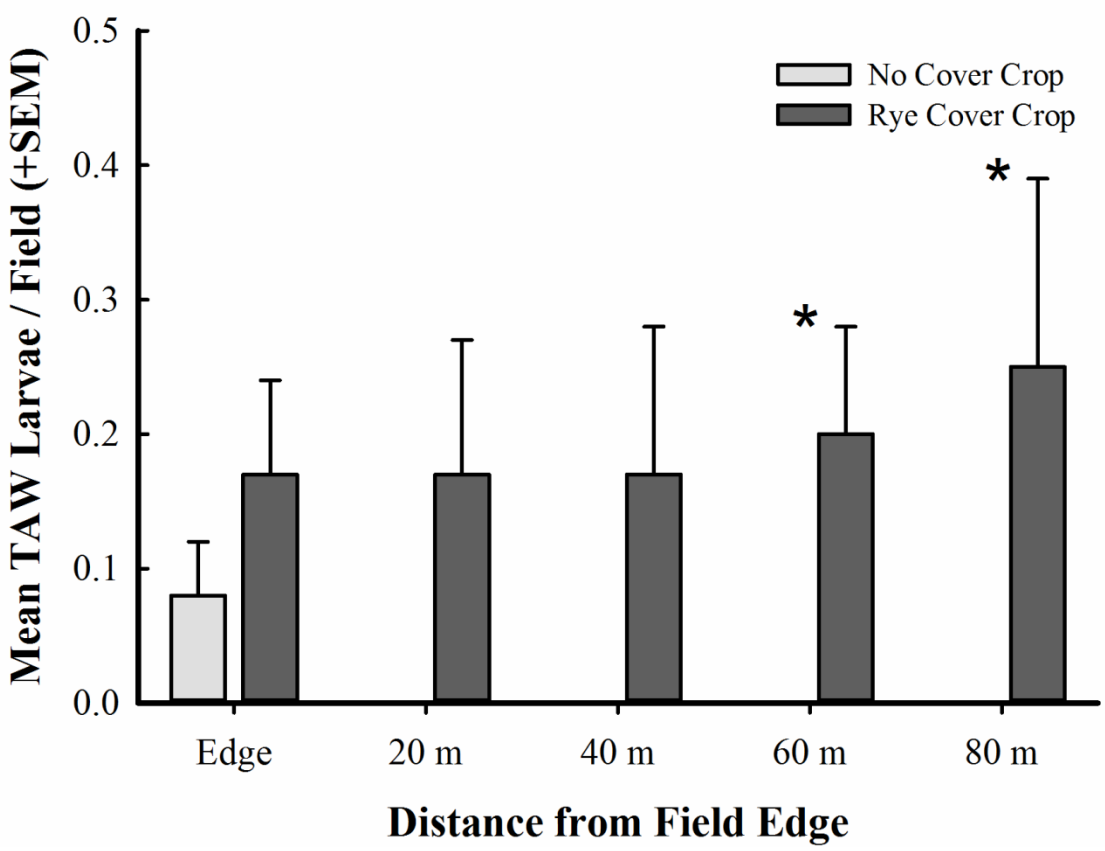

Figure 3A. True armyworm (TAW) (A) and common stalk borer (CSB) (B) larvae captured along transects. Data were combined from 2014 and 2015. Bar heights represent sample means and error bars are the standard error of the means. Stars represent a significant difference in larval abundance between cornfields with and without a rye cover crop at a specific distance along transects.

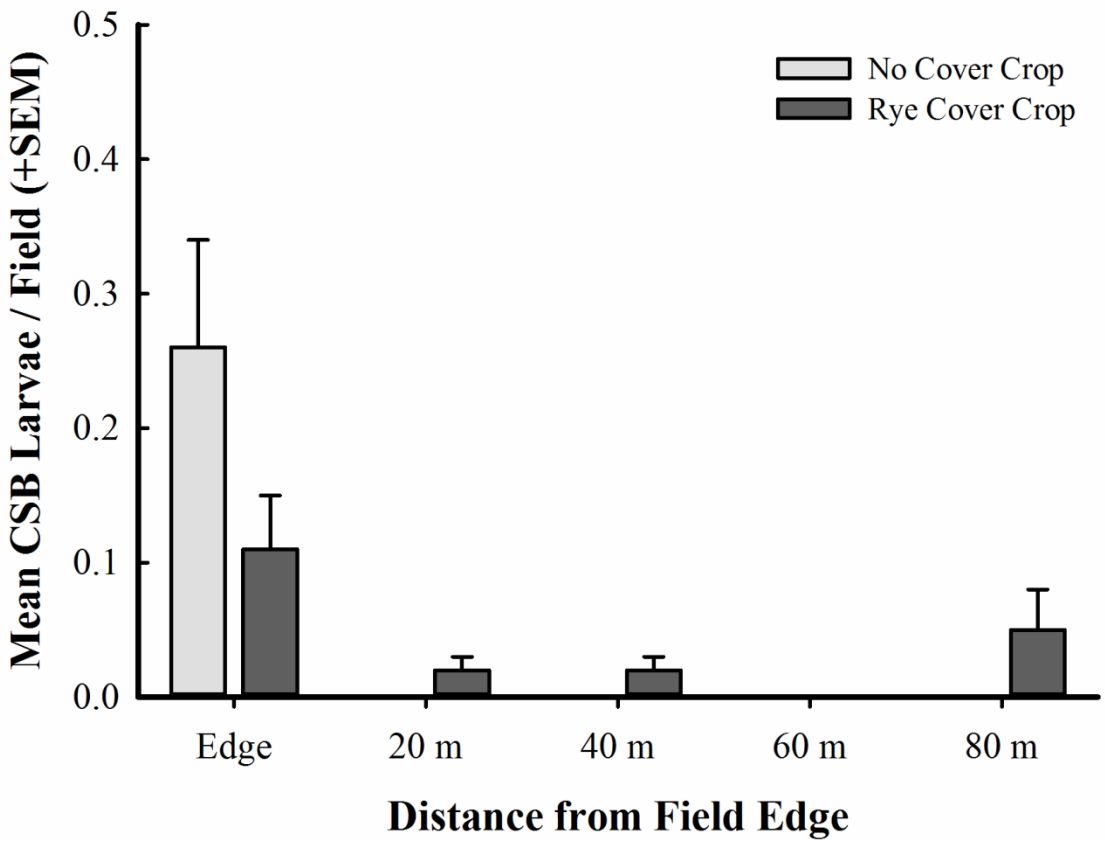

Figure 3B. True armyworm (TAW) (A) and common stalk borer (CSB) (B) larvae captured along transects. Data were combined from 2014 and 2015. Bar heights represent sample means and error bars are the standard error of the means. Stars represent a significant difference in larval abundance between cornfields with and without a rye cover crop at a specific distance along transects.

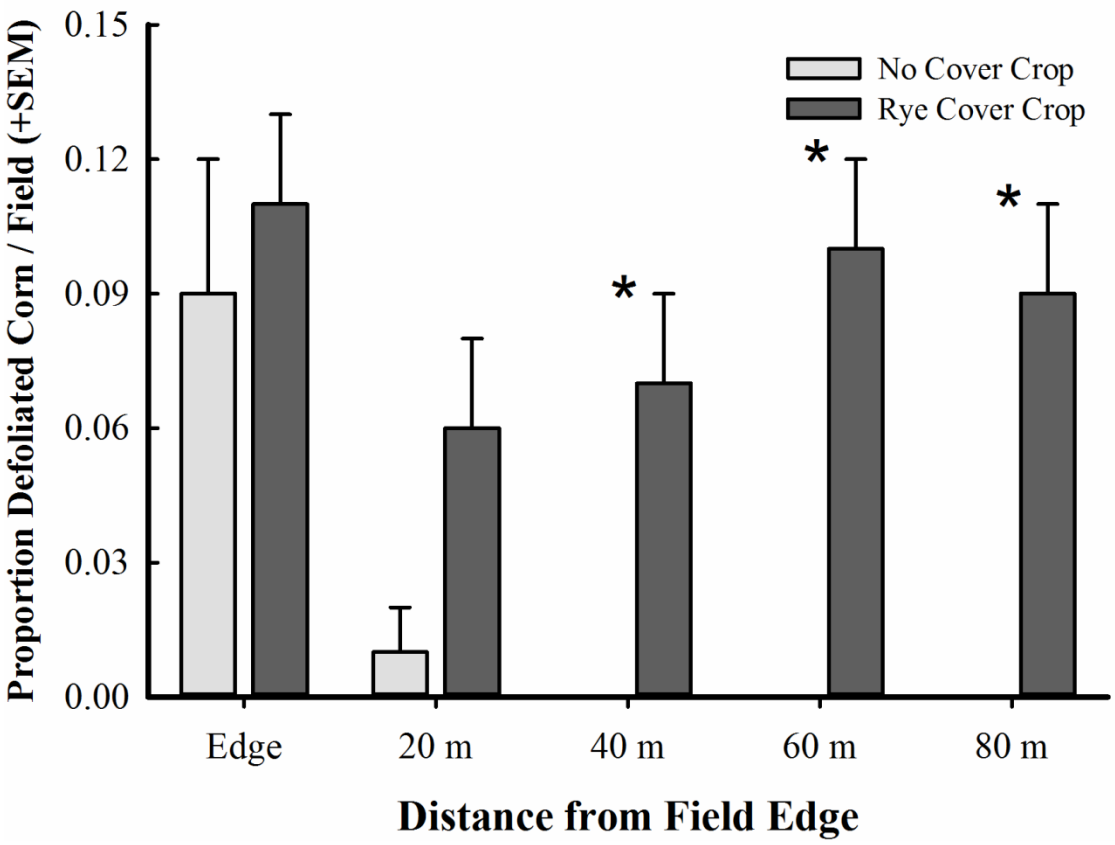

Figure 4. Proportion of defoliated corn plants by distance along transects. Data were combined from 2014 and 2015. Bar heights represent sample means and error bars are the standard error of the means. Stars represent a significant difference in injury between cornfields with and without a rye cover crop at a specific distance along transects.

CHAPTER 6.

GENERAL CONCLUSIONS

The objectives of this dissertation were to test the effect of farming practices that alter vegetational diversity on beneficial arthropod communities and pest insects. In four separate experiments, our findings suggest that the effect of altering vegetational diversity within agroecosystems on arthropods will depend on the agronomic practice and taxon. The objective of Chapter 2 was to quantify the effects of a rye cover crop planted within annually rotated corn and soybean on the composition and abundance of both epigeal and canopy beneficial arthropods. Most taxa did not respond significantly to the presence of the rye cover crop when analyzed individually, although epigeal predators in soybean plots responded positively to the presence of the rye cover crop. The enemies hypothesis predicts that natural enemies would be found in greater abundances in agroecosystems with greater vegetational diversity compared to those lacking diversity, and data presented here support the enemies hypothesis. However, the extent to which the greater presence of predators in soybean following a rye cover crop would reduce pest pressure remains unknown.

The goal of Chapter 3 was to quantify the effect of rotation schemes that vary in the diversity of crops planted on the composition of epigeal, beneficial arthropods. Rotation schemes sampled included continuous corn, annually rotated corn and soybean, and an extended rotation of corn, soybean, and wheat. We predicted that rotation schemes that included greater crop diversity would positively affect beneficial arthropod communities and individual taxa, however rotation schemes had no effect on the community composition or any individual taxa. The lack of effect of rotations schemes on beneficial arthropods, as well

as the modest differences observed Chapter 2, may be partially explained by the fact that these farming practices were all composed of annual crops. Annual crops are associated with agricultural practices that make infield habitat subject to anthropogenic disturbances and temporally unstable, which can limit the effectiveness and retention of beneficial arthropods. Increasing non-crop and perennial species within agroecosystems in conjunction with more diverse farming practices may increase the benefits associated with more robust natural enemy communities.

Diabrotica virgifera virgifera and *D. barberi* are serious pests of corn in the U. S. In Chapter 4, we tested the effects of field history, including crop rotation and management of *Diabrotica* spp., on root injury and abundance of adult *D. v. virgifera* and *D. barberi*, and hypothesized that root injury and adult abundance would be reduced in fields with more diverse field histories compared to fields that lack diverse cropping history. Interestingly, root injury and abundance of *D. v. virgifera* did not differ among recently rotated fields, continuous cornfields and past problem fields. Comparisons of field histories showed that low root injury and adult abundance in recently rotated fields were achieved with significantly less management inputs compared to continuous cornfields and past problem fields. Current problem fields and continuous cornfields had similar field histories, except that continuous cornfields applied soil insecticides more frequently. Farmers of past problem fields were mitigating the risk of future injury by planting more pyramided Bt corn and applying soil insecticides. These results suggest that greater cropping practice diversity can reduce management inputs for *Diabrotica* spp., however, the effect of cropping practice diversity on resistance evolution remain undetermined.

In Chapter 5, we compare the abundance of early season insect pests and injury to corn from fields with and without a rye cover crop on commercial farms. Unlike the previous studies, here we predicted that the addition of a rye cover crop to cornfields would increase the abundance pest species, especially polyphagous species whose host range included rye. Cornfields that included a rye cover crop had significantly more *Mythimna unipuncta* larvae and defoliation injury to corn compared to cornfields without rye cover crop. The abundance of other polyphagous pests, including *Agrotis ipsilon* and *Papaipema nebris*, did not differ between cornfields with or without a rye cover crop. Farmers planting corn following a rye cover crop should be aware of the potential for increased presence of *M. unipuncta* and for greater injury to corn. Since *M. unipuncta* outbreaks are sporadic, prophylactic management tactics are likely not cost effective. Rather, farmers should scout young, vegetative corn and apply insecticides when *M. unipuncta* populations exceed economic thresholds.